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Species compositions of elasmobranchs caught by three different commercial fishing methods off southwestern Australia, and biological data for four abundant bycatch species

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Abstract—Commercial catches taken in southwestern Australian waters by trawl fisheries targeting prawns and scallops and from gillnet and longline fisheries targeting sharks were sampled at different times of the year between 2002 and 2008. This sampling yielded 33 elasmobranch species representing 17 families. Multivariate statistics elucidated the ways in which the species compositions of elasmobranchs differed among fishing methods and provided benchmark data for detecting changes in the elasmobranch fauna in the future. Virtually all elasmobranchs caught by trawling, which consisted predominantly of rays, were discarded as bycatch, as were approximately a quarter of the elasmobranchs caught by both gillnetting and longlining. The maximum lengths and the lengths at maturity of four abundant bycatch species, *Heterodontus portusjacksoni*, *Aptychotrema vincentiana*, *Squatina australis*, and *Myliobatis australis*, were greater for females than males. The L_{50} determined for the males of these species at maturity by using full clasper calcification as the criterion of maturity did not differ significantly from the corresponding L_{50} derived by using gonadal data as the criterion for maturity. The proportions of the individuals of these species with lengths less than those at which 50% reach maturity were far greater in trawl samples than in gillnet and longline samples. This result was due to differences in gear selectivity and to trawling being undertaken in shallow inshore waters that act as nursery areas for these species. Sound quantitative data on the species compositions of elasmobranchs caught by commercial fisheries and the biological characteristics of the main elasmobranch bycatch species are crucial for developing strategies for conserving these important species and thus the marine ecosystems of which they are part.

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The impact of commercial fisheries on the populations of sharks and rays has, in recent years, become an issue of international concern (Stevens et al., 2000; Walker et al., 2005). It is important to recognize, however, that elasmobranchs are not only targeted by certain fisheries, but also comprise a substantial component of the bycatch of commercial fisheries, such as those employing trawl nets, gillnets, and longlines (Stevens et al., 2000; Stobutzki et al., 2001; Walker, 2005a). An assessment of the impacts of commercial fishing on the elasmobranchs taken as bycatch is hindered by the fact that most of that catch is typically reported as "unidentified shark" or "mixed fish," or not reported at all (Walker, 2005a). The numbers of sharks and rays taken as bycatch by commercial fisheries may, in some cases, exceed those of the targeted species, and many of those individuals die either during capture or after they are discarded (Bonfil, 1994; Stobutzki et al., 2002; Walker, 2005a). Although, in most studies of commercial fisheries, nontargeted species are referred to as bycatch, Walker et al. (2005) emphasized that some of those species are usually retained and thus constitute byproduct, whereas the others are usually discarded and therefore constitute bycatch in the strict sense.

In an assessment of various commercial fisheries throughout the world, it was shown that trawl fisheries targeting prawns generate the largest amount of bycatch (Cook, 2003) and that the mortality of individuals in that bycatch is substantial (Bonfil, 1994). Indeed, it has been estimated that approximately two thirds of the elasmobranchs caught as bycatch in Australia's northern prawn trawl fishery die while in the net (Stobutzki et al., 2002). Furthermore, that study demonstrated that most of these individuals are small, and more than half are immature and some are caught immediately after birth.

Many elasmobranchs are at or near the apex of marine food webs and thus their removal can have a significant impact on the trophic structure of an ecosystem (Camhi et al., 1998; Stevens et al., 2000; Shepard and Myers, 2005). Furthermore, certain biological characteristics of elasmobranchs, such as their long life spans, low fecundities, and late ages at maturity, limit their ability both to withstand fishing pressure, either when targeted or caught incidentally, and to recover from overexploitation (Stevens et al., 2000; Walker, 2005a; Gallucci et al., 2006). In general, the populations of endemic species or those that have localized distributions tend to be most prone to overfishing (Stevens et al., 2000). Moreover, there are little or no data on the reproductive biology of most bycatch species. Such data are required for determining the resilience of these species to fishing pressure, thereby enabling the development of manage-

ment plans for conserving their populations (Frisk et al., 2001; Stobutzki et al., 2002; Walker, 2005b).

Most of the species in Australia's rich diversity of elasmobranchs are endemic and occupy demersal habitats on the continental shelf or slope (Last and Stevens, 2009) and are thus potentially prone to depletion by demersal fishing methods such as trawling, gillnetting, and longlining (Stobutzki et al., 2001, 2002; Coelho et al., 2003; Perez and Wahrlich, 2005, Walker et al., 2005). Analyses of fisheries data for 1994 to 1999 showed that the bycatch species *Heterodontus portusjacksoni* (Heterodontidae) and *Myliobatis australis* (Myliobatidae) are abundant in catches of the temperate demersal gillnet and longline fisheries of southwestern Australia (McAuley and Simpfendorfer, 2003). These two species and the rhinobatid *Aptychotrema vincentiana* and the squatinid *Squatina australis*, which are also caught as bycatch by commercial fisheries, collectively contributed as much as 17% to the total biomass of the 172 species of fish caught during extensive trawling along the lower west coast of Australia (Hyndes et al., 1999). It has been estimated that approximately half of the elasmobranchs taken as bycatch by commercial trawlers in this region are likely to die during or after capture (Laurenson et al.[1]). Despite the potentially detrimental effects of commercial fishing on the above four elasmobranch species and their ecological importance in the temperate waters of southern Australia, sound biological data have been collected only for *H. portusjacksoni* (McLaughlin and O'Gower, 1971; Tovar-Ávila et al., 2007; Jones et al., 2008; Powter and Gladstone, 2008).

The families to which the above four species belong are represented elsewhere in the world by species that are taken in substantial numbers as bycatch. For example, in the eastern Pacific, up to a thousand individuals of the heterodontid shark *Heterodontus mexicanus* may be caught in a single gillnet set, many of which die (Garayzar, 2006). In some parts of the world, the populations of several species of rhinobatid and squatinid have been so drastically depleted from overfishing that they have been listed as critically endangered (Morey et al., 2006; Lessa and Vooren, 2007). In eastern Australia, the commercial landings of *Myliobatis australis* have been steadily increasing to the point where their stocks now need to be monitored (White et al., 2006).

The first aim of the present study was to determine the numbers, and thereby the percent contributions, of the females and males of each shark and ray species in samples of commercial catches taken in southwestern Australian waters by demersal trawling for prawns and scallops and by demersal gillnetting and longlining for sharks. These data enabled the percent contributions made by the bycatch and byproduct to the total elasmobranch catch to be estimated for each fishing method. The percent contributions of each species to the catches obtained by trawling, gillnetting, and longlining were then used to compare statistically the species compositions of the elasmobranchs in the catches taken by each of these fishing methods.

Emphasis was next placed on determining the length compositions of the bycatch species *H. portusjacksoni*, *A. vincentiana*, *S. australis*, and *M. australis* in samples collected by trawling, gillnetting, and longlining and on estimating the lengths at maturity of the last three of these ecologically important species. The lengths of both the females and males at which 50% are mature (L_{50}) were first determined by using gonadal data as the criterion for determining maturity and then, in the case of males, by employing full clasper calcification as that criterion. The L_{50} calculated for the males of each species by using the two maturity criteria were then compared to ascertain whether the L_{50} derived by using clasper calcification as the index of maturity is a reasonable proxy for that derived using gonadal stage as that criterion. The L_{50} at maturity of *A. vincentiana*, *S. australis*, and *M. australis* and of *H. portusjacksoni* (Jones et al., 2008) were then employed to determine the proportions of both sexes of each of these four species that were caught by each fishing method before they had the opportunity to reproduce. Finally, the management and conservation implications of our data are considered.

Materials and methods

Sampling regime

The elasmobranchs were examined in commercial catches from 69 demersal trawls, 24 demersal gillnets, and 19 longline sets of fishing vessels operating in southwestern Australian waters southwards of 32° S lat. on the west coast and then eastwards to 118° E long. on the south coast (Fig. 1). Trawling targets the western king prawn (*Melicertus latisulcatus*) and the Ballot's saucer scallop (*Amusium balloti*), whereas demersal gillnetting and longlining target mainly the gummy shark (*Mustelus antarcticus*), the dusky shark (*Carcharhinus obscurus*), and the whiskery shark (*Furgaleus macki*) (McAuley and Simpfendorfer, 2003). Sampling, which was undertaken between November 2002 and November 2008, was designed to ensure that the catches of each fishing method were sampled at least once, and generally on at least three occasions, in each season of the calendar year. The trawl, gillnet, and longline fishermen, whose catches were selected for sampling, were those that fished regularly and readily allowed us onboard, and whose methods were representative of those used in the area that is fished. The numbers of each elasmobranch species caught by each fishing method on each sampling occasion were recorded, as also were the sexes of all individuals except for those of a few species in a small number of trawl samples when the catches of those species were particularly large, in which case the sexes of

[1] Laurenson, L. J. B., P. Unsworth, J. W. Penn, and R. C. J. Lenanton. 1993. The impact of trawling for saucer scallops and western king prawns on the benthic communities in coastal waters off south-western Australia, 93 p. Fisheries Res. Report, Department of Fisheries, no.100 (part 1), Western Australia.

each individual in a large, randomly selected subsample were recorded. Each elasmobranch species caught by gillnetting and longlining was categorized as either targeted, byproduct, or bycatch, whereas those taken by trawling, where prawns and scallops are the target species, were categorized as either byproduct or bycatch.

Trawling was undertaken mainly at depths of 8 to 13 m in a marine embayment on the lower west coast of Western Australia and, to a lesser extent, at depths ≤32 m and at distances within 20 km from the mainland along that coast. The trawl net, in which the codend consisted of 45-mm mesh, was towed for 60–180 min at a speed of ~6.5 km/h. Commercial gillnet fishermen deployed up to 7000 m of either 165- or 178-mm stretched mesh net that was set for up to 24 hours at depths of 24–73 m, whereas longlines, consisting of 360 hooks attached to approximately 6400 m of mainline, were set for an average of 3 hours at depths of 65–73 m.

Multivariate analysis

The square root of the percent contribution of the number of each elasmobranch species to the total catch of all elasmobranchs recorded in each sample during regular onboard observations of the catches taken by each fishing method was used to construct a Bray-Curtis similarity matrix, which was then subjected to nonmetric multidimensional scaling (nMDS). One-way analysis of similarities (ANOSIM) was used to test whether the species compositions of the elasmobranch catches taken by the three fishing methods were significantly different and, if so, pair-wise ANOSIM tests were used to test for differences between the compositions of the elasmobranchs obtained by each pair of methods. The *R*-statistic value was then employed to ascertain the extent of any differences between the compositions of those catches (Clarke, 1993). *R*-statistic values approaching 1 demonstrate that the species composition of the *a priori* groups differed markedly, and a value of approximately 0 indicates that the species compositions of those groups are very similar. Similarity percentages (SIMPER; Clarke, 1993) were used to identify the species that typify the samples obtained by each fishing method and which species are responsible for discriminating between the samples caught by each pair of methods. The ordination and associated tests were undertaken with the PRIMER vers. 6 statistical package (Clarke and Gorley, 2006).

Length and weight measurements

A randomly selected subset of individuals collected during regular onboard observations, together with additional randomly selected individuals provided by commercial fishermen, yielded a total of 516 *H. portusjacksoni*, 340 *A. vincentiana*, 362 *S. australis*, and 218 *M. australis*, which were brought to the laboratory and processed. The data derived from the samples were used to construct length-frequency histograms and to derive sex ratios and reproductive data for the species. The sex of each individual was recorded and the total length

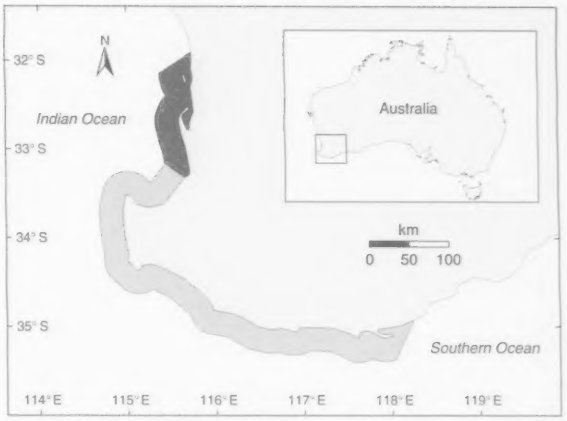

Figure 1

Map showing the region between the northernmost and easternmost limits of southwestern Australia from which elasmobranchs were recorded onboard commercial trawling (dark gray area) and gillnetting and longlining vessels (light and dark gray areas).

(*TL*—tip of snout to tip of tail) and total weight (*W*) of each *H. portusjacksoni*, *A. vincentiana* and *S. australis* were measured and weighed to the nearest 1 mm and 1 g, respectively. The disc length (*DL*— tip of snout to the junction of the tail and pelvic fins) of each *M. australis* was measured to the nearest 1 mm and the disc width (*DW*) and weight of each fully intact individual were recorded to the nearest 1 mm and 1 g, respectively. The relationships between *DW* and *DL*, *DL* and *DW*, and between the natural logarithms of *W* and *DL* and of *W* and *DW* for intact *M. australis* were calculated by using least trimmed squares (LTS) regression. A resampling test was used to demonstrate that the above data for the two sexes could be pooled. The above relationships were used to estimate the *DW* and *W* of the small number of *M. australis* (~15%) whose pectoral fins had been removed by fishermen for commercial sale. Note that, in the results, the sample size (n) and coefficient of determination (r^2) refer to the trimmed data for the individuals used for the analyses.

Length at maturity

The reproductive tracts of the females and males of *A. vincentiana*, *S. australis*, and *M. australis* were assigned to one of the following maturity stages by using the criteria outlined in White et al. (2001). For females, stage 1 = uteri small and thin and oocytes not macroscopically visible; stage 2 = uteri enlarging but still thin and oocytes becoming visible but not yet containing yolk; stage 3 = uteri enlarged and oocytes yolked; stage 4 = pregnant, and stage 5 = uteri or cloaca distended, indicating that parturition had recently occurred. For males, stage 1 = seminal vesicles small and thin and testes not well defined; stage 2 = seminal vesicles enlarging and starting to become coiled, but testes not yet lobed; stage 3 =

seminal vesicles tightly coiled and testes lobed; and stage 4 = similar to stage 3, but with semen present in the distal portion of the seminal vesicle. Individuals with reproductive tracts at stages 1 and 2 are regarded as sexually immature, whereas those at stages 3 and 4 and, in females, also at stage 5, can reproduce or have reproduced and are therefore considered mature. When we alternatively employed full clasper calcification as the indicator of maturity, we considered that males with noncalcified and partially calcified claspers were sexually immature, and those with fully calcified claspers were mature because they have the ability to copulate.

The probability (P) that an individual is mature was assumed to be a logistic function of its length (L):

$$P = \left\{1 + \exp\left[-(\alpha + \beta L)\right]\right\}^{-1}, \quad (1)$$

where α and β are parameters that determine the location and shape of the logistic curve.

The parameters α and β were transformed to the lengths L_{50} (TL_{50} or DL_{50}) and L_{95} (TL_{95} or DL_{95}) by which 50% and 95% of fish have attained maturity, respectively, using the equations

$$L_{50} = -\alpha / \beta, \quad (2)$$

$$L_{95} = \left[\log_e(19) - \alpha\right]/\beta. \quad (3)$$

The equation for the probability that a fish is mature thus becomes

$$P = \left\{1 + \exp\left[-\log_e(19)(L - L_{50})/(L_{95} - L_{50})\right]\right\}^{-1}. \quad (4)$$

Logistic relationships of the above form were derived for females and males of *A. vincentiana*, *S. australis*, and *M. australis* by using gonadal maturity status, i.e., ≥stage 3, as the criterion for maturity and, in addition, for males, employing full clasper calcification as the criterion for maturity. Logistic regression analysis was used to fit these logistic curves by using Solver in Excel (Microsoft, Redmond, WA) to maximize the log-likelihood. We used likelihood-ratio tests (Cerrato, 1990) to compare the L_{50} of the females and males of each species at maturity using gonadal status as the criterion for maturity and to compare the L_{50} derived for males using both gonadal and clasper calcification status as the criteria for maturity. For the likelihood-ratio tests, the hypothesis that the data for both the females and males of each species could be described by a common logistic curve was rejected at the α=0.05 level of significance if the test statistic, calculated as twice the difference between the log-likelihoods obtained by fitting maturity curves with a common value of L_{50} for both sexes and by fitting separate maturity curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two approaches. Note that the L_{50} of females and males of *H. portusjacksoni* at maturity had been determined previously with this approach (Jones et al., 2008). WinBUGS (Lunn et al., 2000) was also used to fit the logistic curves to the maturity-at-length data for the females and males of each species and to calculate the proportion that were mature at length, thereby enabling derivation of the upper and lower confidence intervals for the L_{50} and L_{95} values and for the proportion of mature males and females in each 50-mm length class (see Jones et al. [2008] for further details of this WinBUGS analysis).

Results

Species compositions by fishing method

A total of 4820 individual elasmobranchs, representing 10 families and 22 species of sharks and 7 families and 11 species of rays, were recorded during regular onboard examinations of the catches of commercial trawl, gillnet, and longline vessels operating off the southwestern coast of Australia (Tables 1–3).

The 2986 elasmobranchs caught by prawn and scallop trawling were dominated by rays, which comprised 10 of the 14 species and contributed 87% to the total elasmobranch catch (Table 1). The species of a single family of rays, the Urolophidae, comprising four species and two genera, contributed as much as 67% to the total trawl catch of elasmobranchs. The two species of shark (*H. portusjacksoni* and *S. australis*) and the two species of ray (*A. vincentiana* and *M. australis*), whose biological characteristics were determined (see later), each contributed between 4.5% and 8% to the total number of elasmobranchs caught by trawling and collectively as much as 25% (Table 1). Two species of shark, *M. antarcticus* and *C. brevipinna*, which were caught in very small numbers, were retained and thus constituted byproduct.

Gillnet catches yielded 1260 elasmobranchs, representing 19 species of shark and 6 species of ray, with sharks contributing 96% to the total catch of elasmobranchs (Table 2). The most abundant species in the gillnet catches was a targeted shark, *Carcharhinus obscurus*, which contributed more than a third to the total elasmobranch catch. The other two targeted species, *Mustelus antarcticus* and *Furgaleus macki*, which were dominated by females, ranked third and fifth in terms of abundance, respectively, and contributed an additional 14.2% and 6.5%, respectively (Table 2). The second most numerous species, however, was the shark *H. portusjacksoni*, a bycatch species, which constituted one-fifth of the total catch. None of the six species of ray caught by gillnetting was abundant in the catches obtained by this method. The byproduct and bycatch species contributed 18.7% and 25.7%, respectively, to the total gillnet catch. Thirteen of these species, which contributed more than one third to the total number of individuals of elasmobranchs caught, were always discarded as bycatch.

The 22 species of elasmobranch caught by longlining were dominated by one of the three targeted species, *M. antarcticus*, which made up 63% of the total catch of 574 individual elasmobranchs (Table 3). The next four most

Table 1

Number of females and males and percentage contribution of females of each elasmobranch species (sex determined during regular onboard observations) in the catches of trawl vessels fishing for prawns and scallops on the lower west coast of Australia. The total number of individuals of each species (including those whose sex could not be determined owing to logistic constraints) and the percent contribution of each species to the total elasmobranch catch are also given. Plain font* = byproduct species, i.e., those that are not targeted but usually retained; Bold font = bycatch species, i.e., those that are usually discarded.

Common name	Species name	Female *n*	Male *n*	Female %	Total *n*	Total %
Lobed stingaree	***Urolophus lobatus***	422	288	59.4	851	28.5
Sparsely-spotted stingaree	***Urolophus paucimaculatus***	235	349	40.2	726	24.3
Masked stingaree	***Trygonoptera personata***	84	66	56.0	277	9.3
Western shovelnose ray	***Aptychotrema vincentiana***	124	99	55.6	237	7.9
Port Jackson shark	***Heterodontus portusjacksoni***	112	110	50.5	223	7.5
Southern fiddler ray	***Trygonorrhina dumerilii***	94	118	44.3	220	7.4
Western shovelnose stingaree	***Trygonoptera mucosa***	23	27	46.0	153	5.1
Southern eagle ray	***Myliobatis australis***	67	81	45.3	148	5.0
Australian angelshark	***Squatina australis***	67	66	50.4	135	4.5
Smooth stingray	***Dasyatis brevicaudata***	2	6	25.0	8	0.3
Gummy shark*	*Mustelus antarcticus**	4	1	80.0	5	0.2
White-spotted guitarfish	***Rhynchobatus australiae***	1	0	100.0	1	< 0.1
Spinner shark*	*Carcharhinus brevipinna**	0	1	0	1	< 0.1
Coffin ray	***Hypnos monopterygius***	0	1	0	1	< 0.1
Total		1235	1213		2986	

abundant species, which were all bycatch, consisted of three species of rays and the shark *H. portusjacksoni* and collectively contributed nearly a quarter of the individual elasmobranchs obtained by longlining. The other two targeted species, *C. obscurus* and *F. macki*, contributed only 3.8% and 0.9%, respectively, to the total catch taken by longlining. The 19 nontargeted species caught by longlining comprised eight species that were always discarded as bycatch and represented one quarter of the total catch.

On the ordination plot, derived from the similarity matrix constructed by using percent contributions of the various species to the elasmobranch catches obtained by the three fishing methods, the samples for longlining lie above those for gillnetting, and both of these lie to the right of the discrete group comprising the trawl samples (Fig. 2). One-way ANOSIM confirmed that the compositions of the samples obtained by the three fishing methods were significantly different (P=0.001, global R=0.753). Pair-wise ANOSIM tests revealed that the compositions in the samples collected by each method differed significantly from those in the samples obtained by each other method (all P<0.001), and the R-statistic was similarly high for trawling vs. gillnetting (0.797) and trawling vs longlining (0.774) and greater than that for gillnetting vs longlining (0.515).

The most important of the typifying species for the trawl samples, i.e., those that were most abundant and were found most frequently, comprised two ray species, *A. vincentiana* and *Urolophus paucimaculatus*, and two shark species, *H. portusjacksoni* and *S. australis* (Table 4). *Heterodontus portusjacksoni* and *M. antarcticus* were also important typifying species for the elasmobranch catches taken by both gillnetting and longlining. *Carcharhinus obscurus* is a particularly important typifying species for the gillnet samples and the same is true for the bycatch ray species *Dasyatis brevicaudata* for the longline samples. Relatively greater

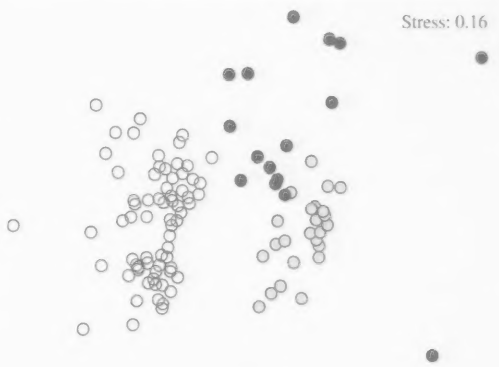

Figure 2

Nonmetric multidimensional scaling (nMDS) ordination plot, derived from the matrix constructed from the percentage contribution (square root transformed) of each elasmobranch species recorded during each of the regular onboard observations of the catches of commercial trawling (open circles), gillnetting (gray circles), and longlining vessels (black circles).

Table 2

Number of females and males, percent contribution of females, and the total number and percent contributions of each elasmobranch species that were recorded during regular onboard observations of catches from gillnet vessels on the southwest coast of Australia. Plain font = targeted species; Plain font* = byproduct species i.e., those species not targeted but usually retained; Bold font = bycatch species, i.e., those species that are usually discarded.

Common name	Species name	Female *n*	Male *n*	Female %	Total *n*	Total %
Dusky shark	*Carcharhinus obscurus*	229	208	52.4	437	34.7
Port Jackson shark	***Heterodontus portusjacksoni***	131	120	52.2	251	19.9
Gummy shark	*Mustelus antarcticus*	151	28	84.4	179	14.2
Sandbar shark*	*Carcharhinus plumbeus**	86	59	59.3	145	11.5
Whiskery shark	*Furgaleus macki*	69	13	82.9	82	6.5
Southern eagle ray	***Myliobatis australis***	18	14	56.3	32	2.5
Spinner shark*	*Carcharhinus brevipinna**	17	8	68.0	25	2.0
Western wobbegong*	*Orectolobus hutchinsi**	7	11	38.9	18	1.4
Gulf wobbegong*	*Orectolobus halei**	3	12	20.0	15	1.2
Smooth hammerhead*	*Sphyrna zygaena**	8	4	66.7	12	1.0
Cobbler wobbegong	***Sutorectus tentaculatus***	7	4	63.6	11	0.9
Bronze whaler*	*Carcharhinus brachyurus**	10	1	90.9	11	0.9
Spotted wobbegong*	*Orectolobus maculatus**	2	7	22.2	9	0.7
Western shovelnose ray	***Aptychotrema vincentiana***	2	4	33.3	6	0.5
Australian angelshark	***Squatina australis***	2	4	33.3	6	0.5
Common sawshark	***Pristiophorus cirratus***	4	1	80.0	5	0.4
Southern fiddler ray	***Trygonorrhina dumerilii***	3	2	60.0	5	0.4
Grey nurse shark	***Carcharias taurus***	2	0	100.0	2	0.2
Lobed stingaree	***Urolophus lobatus***	1	1	50.0	2	0.2
Floral banded wobbegong	***Orectolobus floridus***	2	0	100.0	2	0.2
Smooth stingray	***Dasyatis brevicaudata***	1	0	100.0	1	< 0.1
Pencil shark*	*Hypogaleus hyugaensis**	0	1	0.0	1	< 0.1
Ornate angelshark	***Squatina tergocellata***	1	0	100.0	1	< 0.1
Scalloped hammerhead*	*Sphyrna lewini**	0	1	0.0	1	< 0.1
Western shovelnose stingaree	***Trygonoptera mucosa***	0	1	0.0	1	< 0.1
Total		756	504		1260	

and more consistent numbers of *A. vincentiana* were particularly important for discriminating between the compositions of the samples caught by trawling and those obtained by both gillnetting and longlining, and greater and more consistent numbers of *C. obscurus* were especially important for discriminating between the samples taken by gillnetting from those obtained by both trawling and longlining (Table 4). The longline samples were discriminated from those obtained by both trawling and gillnetting by consistently greater numbers of *D. brevicaudata*.

Length-frequency compositions of the four selected bycatch species by fishing method

Wide size ranges of *H. portusjacksoni*, *A. vincentiana*, and *S. australis* and, to a certain extent, *M. australis*, were caught by trawling. However, the lengths of most *H. portusjacksoni* and *M. australis* were small and thus lay toward the lower end of their length ranges (Fig. 3). Although gillnetting also caught a broad size range of both *H. portusjacksoni* and *A. vincentiana*, it yielded predominantly larger *S. australis* and medium-size *M. australis* (Fig. 3). Although longline catches contained a wide size range of *H. portusjacksoni* and *M. australis*, they did not include the smallest individuals of these two species and only one of the *A. vincentiana* caught by this method was small (Fig. 3). No *S. australis* was caught by longlining.

The *H. portusjacksoni* obtained by all three fishing methods ranged from 180 to 1300 mm TL (Table 5), the latter length rarely being exceeded by this species throughout its range (Last and Stevens, 2009). The smallest individuals possessed conspicuous umbilical scars and were therefore neonates. The length-frequency distribution of female *H. portusjacksoni* is trimodal, whereas that of males is bimodal, and these modes correspond to the first two modes of females (Fig. 4). These differences account for the lengths of many females greatly exceeding the maximum length of 815 mm for males (Table 5). The weights of *H. portusjacksoni* ranged from 39 to 12,250 g (Table 5). The

Table 3

Number of females and males, percent contribution of females and the total number and percent contributions of all individuals of each elasmobranch species that were recorded during regular onboard observations of the catches from longline vessels on the southwest coast of Australia. Plain font = targeted species; Plain font* = byproduct species, i.e., those that are not targeted but usually retained; Bold font = bycatch species, i.e., those species that are usually discarded.

Common name	Species name	Female *n*	Male *n*	Female %	Total *n*	Total %
Gummy shark	*Mustelus antarcticus*	234	129	64.5	363	63.2
Smooth stingray	***Dasyatis brevicaudata***	21	20	51.2	41	7.1
Southern eagle ray	***Myliobatis australis***	15	19	44.1	34	5.9
Southern fiddler ray	***Trygonorrhina dumerilii***	24	8	75.0	32	5.6
Port Jackson shark	***Heterodontus portusjacksoni***	20	11	64.5	31	5.4
Dusky shark	*Carcharhinus obscurus*	16	6	72.7	22	3.8
Smooth hammerhead*	*Sphyrna zygaena**	8	1	88.9	9	1.6
Bronze whaler*	*Carcharhinus brachyurus**	4	1	80.0	5	0.9
Whiskery shark	*Furgaleus macki*	5	0	100.0	5	0.9
Western wobbegong*	*Orectolobus hutchinsi**	1	4	20.0	5	0.9
Common sawshark*	*Pristiophorus cirratus**	4	1	80.0	5	0.9
School shark*	*Galeorhinus galeus**	2	2	50.0	4	0.7
Western shovelnose ray	***Aptychotrema vincentiana***	3	0	100.0	3	0.5
Gulf wobbegong*	*Orectolobus halei**	1	2	33.3	3	0.5
Sandbar shark*	*Carcharhinus plumbeus**	2	0	100.0	2	0.4
Spotted wobbegong*	*Orectolobus maculatus**	0	2	0.0	2	0.4
Rusty carpetshark	***Parascyllium ferrugineum***	0	2	0.0	2	0.4
Melbourne skate	***Spinirija whitleyi***	2	0	100.0	2	0.4
Spinner shark*	*Carcharhinus brevipinna**	0	1	0.0	1	0.2
Australian sawtail catshark	***Figaro boardmani***	1	0	100.0	1	0.2
Pencil shark*	*Hypogaleus hyugaensis**	0	1	0.0	1	0.2
Scalloped hammerhead*	*Sphyrna lewini**	1	0	100.0	1	0.2
Total		364	210		574	

ratio of females to males of *H. portusjacksoni* differed significantly from parity among all individuals collectively (1 female:0.76 males; χ^2=9.46, P<0.01), but not for juveniles (1 female:1.20 males; χ^2=2.65, P>0.05). Note that, when calculating the sex ratios for juveniles, the term juvenile refers to females and males with lengths less than the smallest mature individual of their respective sex.

The *A. vincentiana* caught by all three fishing methods ranged from 201 to 1001 mm *TL* (Fig. 4; Table 5), and the smallest individuals lay within the length range recorded for the embryos of this species (A. Jones, unpubl. data) and the largest individuals exceeded the length of "at least 840 mm" reported for this species by Last and Stevens (2009). The length-frequency distributions of female and male *A. vincentiana* were both broadly bimodal and the numbers of both sexes were relatively low, between 500 and 699 mm (Fig. 4). However, the modal length class of 850–899 mm for the group of large females far exceeded that of 700–749 mm for the group of large males. Furthermore, the largest female *A. vincentiana* was both far longer (1001 mm) and heavier (3634 g) than the largest male, i.e., 872 mm and 1886 g, respectively (Table 5). The ratio of females to males differed significantly from parity among all individuals (1 female:0.67 males; χ^2=12.81, P<0.001), but not among juveniles (1 female:0.76 males; χ^2=3.52, P>0.05).

The smallest *S. australis* caught by all three fishing methods was 228 mm in *TL* (Fig. 4; Table 5) and thus only slightly longer than the length of 220 mm recorded for the largest embryo of this species in a concomitant study (A. Jones, unpubl. data). Although the maximum length of 1004 mm for *S. australis* in our samples is considerably less than the maximum length reported for this species by Last and Stevens (2009), it is still far greater than the TL_{50} for either females or males at maturity in southwestern Australian waters. Although individuals were represented in all 50-mm length classes between 200 and 1049 mm, the length-frequency distributions of females and males were both dominated by their 250–299 mm length classes (Fig. 4). The largest female *S. australis* was far longer (1004 mm) and heavier (10,970 g) than the largest male (859 mm and 5500 g) (Table 5). The ratio of females to males of *S. australis* did not differ significantly from parity among either all individuals collectively (1 female:1.05 males; χ^2=0.18, P>0.05) or among juveniles (1 female:1.11 males; χ^2=0.75, P>0.05).

Table 4

Main species that typified the catches of elasmobranchs recorded onboard trawl, gillnet, and longline vessels (shaded background), and those that discriminate between the catches of elasmobranchs obtained by each pair of fishing methods (unshaded background). Plain font = targeted species; Bold font = bycatch species; * Denotes that the species is relatively more abundant and consistently caught by the sampling method on the top (horizontal) row than on the side (vertical) column.

	Trawl	Gillnet	Longline
Trawl	***Aptychotrema vincentiana*** ***Heterodontus portusjacksoni*** ***Urolophus paucimaculatus*** ***Squatina australis***		
Gillnet	*Carcharhinus obscurus* ***Aptychotrema vincentiana**** ***Heterodontus portusjacksoni*** *Mustelus antarcticus* ***Myliobatis australis**** *Furgaleus macki*	*Carcharhinus obscurus* ***Heterodontus portusjacksoni*** ***Mustelus antarcticus*** ***Furgaleus macki***	
Longline	***Dasyatis brevicaudata*** ***Aptychotrema vincentiana**** ***Trygonorrhina dumerilii**** ***Heterodontus portusjacksoni****	*Carcharhinus obscurus** ***Dasyatis brevicaudata*** *Mustelus antarcticus* ***Heterodontus portusjacksoni**** *Furgaleus macki**	***Dasyatis brevicaudata*** *Mustelus antarcticus* ***Trygonorrhina dumerilii*** ***Heterodontus portusjacksoni***

Table 5

Biological characteristics of four elasmobranch species caught as bycatch by commercial trawl, gillnet, and longline fisheries operating off southwestern Australia. Length measurements are given as total lengths (*TL*) for *Heterodontus portusjacksoni*, *Aptychotrema vincentiana*, and *Squatina australis*, and as disc lengths (*DL*) for *Myliobatis australis*. * denotes a value extrapolated from the regression equation of the relation between *DL* and *W*. The true weight could not be recorded because the pectoral fins had been removed by fishermen. Sample size for each sex of each species is shown on Figure 4.

		Heterodontus portusjacksoni	*Aptychotrema vincentiana*	*Squatina australis*	*Myliobatis australis*
Females	Length range (mm)	198–1300	201–1001	228–1004	118–800
	Weight range (g)	39–12,250	32–3634	94–10,970	117–37,811*
	Smallest mature (mm)	715	754	825	444
	Largest immature (mm)	869	895	834	472
Males	Length range (mm)	180–815	214–872	246–859	129–545
	Weight range (g)	39–3920	33–1886	115–5500	152–12,373*
	Smallest mature (mm)	595	642	754	365
	Largest immature (mm)	654	792	707	433

The relationships between *DW* and *DL* for females and males of *M. australis* collectively are described by the following equations:

$$DW = 1.70\ DL + 8.16\ (r^2=0.997,\ n=96), \quad (5)$$

$$DL = 0.58\ DW - 3.01\ (r^2=0.998,\ n=96). \quad (6)$$

From the values obtained from the above equations, the following relationships between the natural logarithms of *W* and *DL*, and of *W* and *DW* for both sexes are described as

$$\log_e W = 2.91 \log_e DL - 8.92\ (r^2=0.999,\ n=91), \quad (7)$$

$$\log_e W = 3.19 \log_e DW - 12.25\ (r^2=0.999,\ n=91). \quad (8)$$

After correction for bias (Beauchamp and Olson, 1973), the respective back-transformed relationships became

$$W = 0.0001344\ DL^{2.91}, \quad (9)$$

$$W = 0.000004787\ DW^{3.19} \quad (10)$$

The *M. australis* caught by using the three sampling methods ranged from 118 to 800 mm *DL* (Fig. 4, Table 5), which corresponds to 198–1192 mm *DW*. The minimum *DW* is at the extreme lower end of the range reported for this species at birth, and the maximum *DW* is appreciably less than the maximum *DW* of 1600 mm recorded for *M. australis* (Last and Stevens, 2009). The largest female caught was 800 mm *DL* and 37,811 g *W*, which greatly exceeded the 545 mm *DL* and 12,373 g *W* of the largest male (Table 5). Both sexes were represented in each *DL* class between 100 and 549 mm, and females were also present in each subsequent size class up to 800–849 mm (Fig. 4). The length-frequency distributions for both sexes contained a single prominent modal length class at 150–199 mm. The ratio of 1 female:1.27 males of *M. australis* among the individuals caught by all methods collectively did not differ significantly from parity (χ^2=3.10, P>0.05), and the same was true for juveniles, i.e., 1 female:1.04 males (χ^2=0.06, P>0.05).

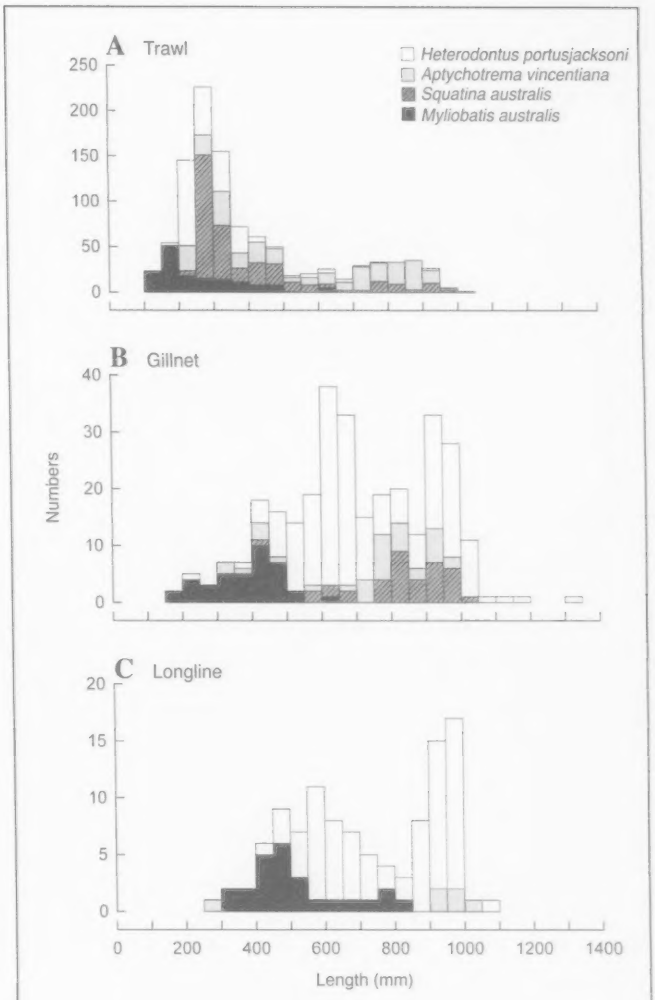

Figure 3

Length-frequency distributions for all males and females of *Heterodontus portusjacksoni*, *Aptychotrema vincentiana*, *Squatina australis*, and *Myliobatis australis* obtained from the commercial catches of (**A**) trawl, (**B**) gillnet, and (**C**) longline vessels. Length refers to total length (*TL*), except in the case of *M. australis* where it refers to disc length (*DL*).

Lengths of females and males at maturity

The smallest female and male of *H. portusjacksoni* with mature gonads measured 715 and 595 mm *TL*, respectively (Table 5). Using gonadal stage as the index, we found that the TL_{50} for female *H. portusjacksoni* at maturity was 805 mm, and the TL_{50} for males was 593 mm, which represent 62% and 73% of their respective maximum *TL*. The TL_{50} for males was only 12 mm greater and not significantly different from the 581 mm derived by using full clasper calcification as the index of maturity (Table 6, see also Jones et al., 2008).

The smallest female and male of *A. vincentiana* with mature gonads were 754 and 642 mm, respectively, and all females ≥896 mm and males ≥793 mm were mature (Fig. 5, Table 5). The TL_{50} for females of 798 mm at maturity differed significantly (P<0.001) from the corresponding TL_{50} for males of 671 mm when using gonadal stage as the criterion for maturity (Table 6). The latter TL_{50} for males did not differ significantly from the TL_{50} of 654 mm derived by using full clasper calcification as the criterion for maturity (P>0.05) (Fig. 5, Table 6). The TL_{50} for female and male *A. vincentiana* at maturity, using gonadal status as the criterion for maturity, were 80% and 77% of their respective maximum *TL*.

On the basis of gonadal data, the *TL* of the smallest mature female and male *S. australis* were 825 and 754 mm, respectively, and all females ≥840 mm and all males ≥754 mm were mature (Fig. 5, Table 5). The TL_{50} for females (823 mm) and males of *S. australis* (734 mm), derived by employing gonadal stage as the criterion for maturity, were significantly different (P<0.001; Table 6). The latter TL_{50} was not significantly different (P>0.05) from the TL_{50} of 721 mm derived for male *S. australis* when using clasper calcification as the criterion for maturity (Fig. 5, Table 6). The TL_{50} calculated for females and males of *S. australis*, with gonadal stage as the criterion for maturity, were 82% and 85% of their respective maximum *TL*.

The *DL* of the smallest females and males of *M. australis* with mature gonads were 444 and 365 mm, respectively, and all females and males with *DL* ≥513 and 433 mm, respectively, were mature (Fig. 5, Table 5). The DL_{50} of 511mm (DW_{50}=879 mm) for females at maturity differed significantly (P<0.001) from the 399 mm (DW_{50}=689 mm) of males when gonadal status was used as the criterion for maturity (Table 6). The latter DL_{50} did not differ significantly (P>0.05) from the 388 mm (DW_{50}=670 mm) derived for males at maturity with clasper calcification as the criterion for maturity (Table 6). On the basis of gonadal criteria, the DL_{50} for females and males of *M. australis* at maturity were 64% and 73% of their DL_{max}, respectively.

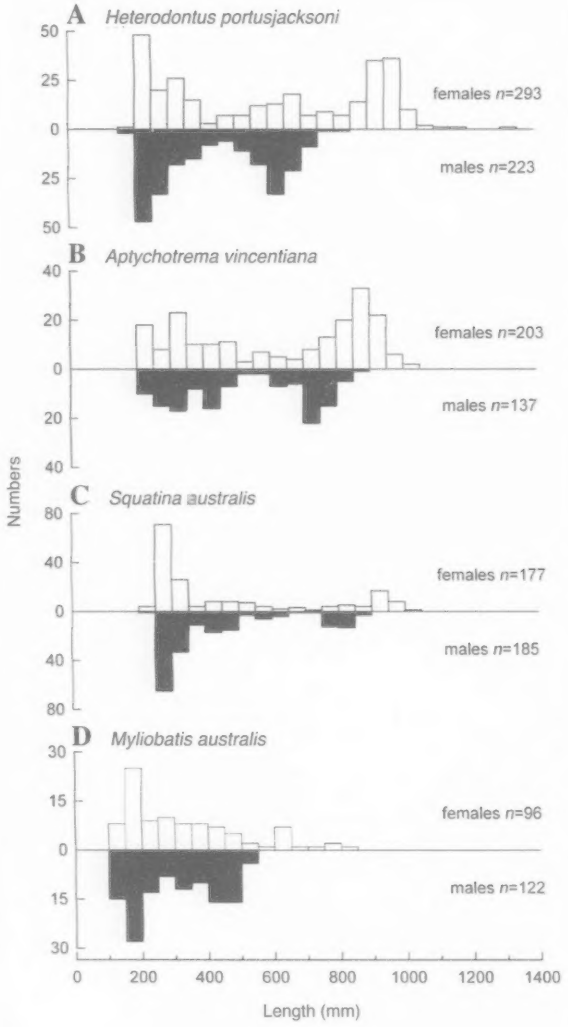

Figure 4

Length-frequency distributions for females (white histograms) and males (black histograms) of (**A**) *Heterodontus portusjacksoni*, (**B**) *Aptychotrema vincentiana*, (**C**) *Squatina australis*, and (**D**) *Myliobatis australis* obtained collectively by all three fishing methods. Length refers to total length (*TL*), except in the case of *M. australis* where it refers to disc length (*DL*).

Percentage of females and males caught by each fishing method

The percentage of females of *H. portusjacksoni*, *A. vincentiana*, *S. australis* and *M. australis* caught in trawls with lengths below the L_{50} (TL_{50} or DL_{50}) at maturity were very high and similar to those of males (Table 7). The percentage in trawl samples of both sexes with lengths less than their L_{50} at maturity ranged from 63% for *A. vincentiana*, to 90% for both *M. australis* and *S. australis*, respectively, to 97% for *H. portusjacksoni* (Table 7). In the case of gillnet samples for three of the four species, the percentage of females with lengths less than their L_{50} at maturity exceeded those of males and particularly so for *M. australis*, for which the values were 86% and 40%, respectively (Table 7). In longline samples, the percentage of males of *H. portusjacksoni* with lengths below their L_{50} at maturity slightly exceeded the corresponding value for females (37% and 32%, respectively).

Discussion

This study is the first to quantify the contribution of each elasmobranch species to the total elasmobranch catch obtained by co-occurring trawl, gillnet, and longline fisheries, and to calculate the contributions made by the bycatch and byproduct species to the catches taken by each fishing method. In addition, our results indicate that nMDS ordination and associated tests would be invaluable for detecting whether the species composition of elasmobranchs in the catch produced by each fishing method changes in the future in response to either variations in fishing activity or environmental factors and, if so, also for elucidating the magnitude of that effect. This study has also produced, for four abundant bycatch species, the sound quantitative biological data of the types required by managers for developing plans for conserving stocks and which are deficient for the vast majority of bycatch species (Stobutzki et al., 2002). The sizes at maturity that were determined for the four bycatch species in this study enabled the proportion of each species, which was caught by each fishing method before it had the potential to reproduce, to be estimated.

Table 6

Estimates of the L_{50} and L_{95} at maturity, and the upper and lower 95% confidence limits (CL), for females and males of *Heterodontus portusjacksoni*, *Aptychotrema vincentiana*, and *Squatina australis* recorded as total length (*TL*). For *Myliobatis australis*, these values were recorded as disc length (*DL*); extrapolated values for disc widths (*DW*) are also provided. Estimates were derived by using gonadal status as an index of maturity for females and males and also by using full clasper calcification as that index for males. Sample sizes for females and males of each species are provided in Figure 4.

		Female (gonads)		Male (gonads)		Male (claspers)	
		L_{50}	L_{95}	L_{50}	L_{95}	L_{50}	L_{95}
Heterodontus portusjacksoni	Estimate	805	896	593	647	581	652
	Upper 95% CL	826	931	605	674	594	689
	Lower 95% CL	781	866	579	628	563	629
Aptychotrema vincentiana	Estimate	798	877	671	766	654	707
	Upper 95% CL	815	920	695	833	676	756
	Lower 95% CL	774	855	631	736	618	679
Squatina australis	Estimate	823	852	734	735	721	723
	Upper 95% CL	842	927	753	806	753	806
	Lower 95% CL	771	826	673	714	674	714
Myliobatis australis	Estimate	511	585	399	472	388	453
	Upper 95% CL	558	696	416	518	404	491
	Lower 95% CL	480	538	376	440	366	420
		Female (gonads)		Male (gonads)		Male (claspers)	
		DW_{50}	DW_{95}	DW_{50}	DW_{95}	DW_{50}	DW_{95}
Myliobatis australis	Estimate	879	1006	689	813	670	781
	Upper 95% CL	960	1195	717	891	697	845
	Lower 95% CL	827	926	649	758	632	724

Table 7

Numbers of females and males and total number of *Heterodontus portusjacksoni*, *Aptychotrema vincentiana*, *Squatina australis*, and *Myliobatis australis* that were caught by each fishing method and examined in the laboratory, and the percentages of individuals with lengths less than their L_{50} at maturity when using gonadal status as the index of maturity. L_{50} refers to total length (TL_{50}), except in the case of *M. australis* where it refers to disc length (DL_{50}).

		Females		Males		Sexes combined	
Fishing method	Species name	n	% < L_{50}	n	% < L_{50}	n	% < L_{50}
Trawl	*Heterodontus portusjacksoni*	121	98	128	96	249	97
	Aptychotrema vincentiana	182	62	116	66	298	63
	Squatina australis	155	89	169	91	324	90
	Myliobatis australis	71	92	83	87	154	90
Gillnet	*Heterodontus portusjacksoni*	115	44	76	30	191	38
	Aptychotrema vincentiana	16	38	20	30	36	33
	Squatina australis	22	18	16	19	38	18
	Myliobatis australis	14	86	25	40	39	56
Longline	*Heterodontus portusjacksoni*	57	32	19	37	76	33
	Aptychotrema vincentiana	5	0	1	100	6	17
	Squatina australis	—	—	—	—	—	—
	Myliobatis australis	11	36	14	7	25	20

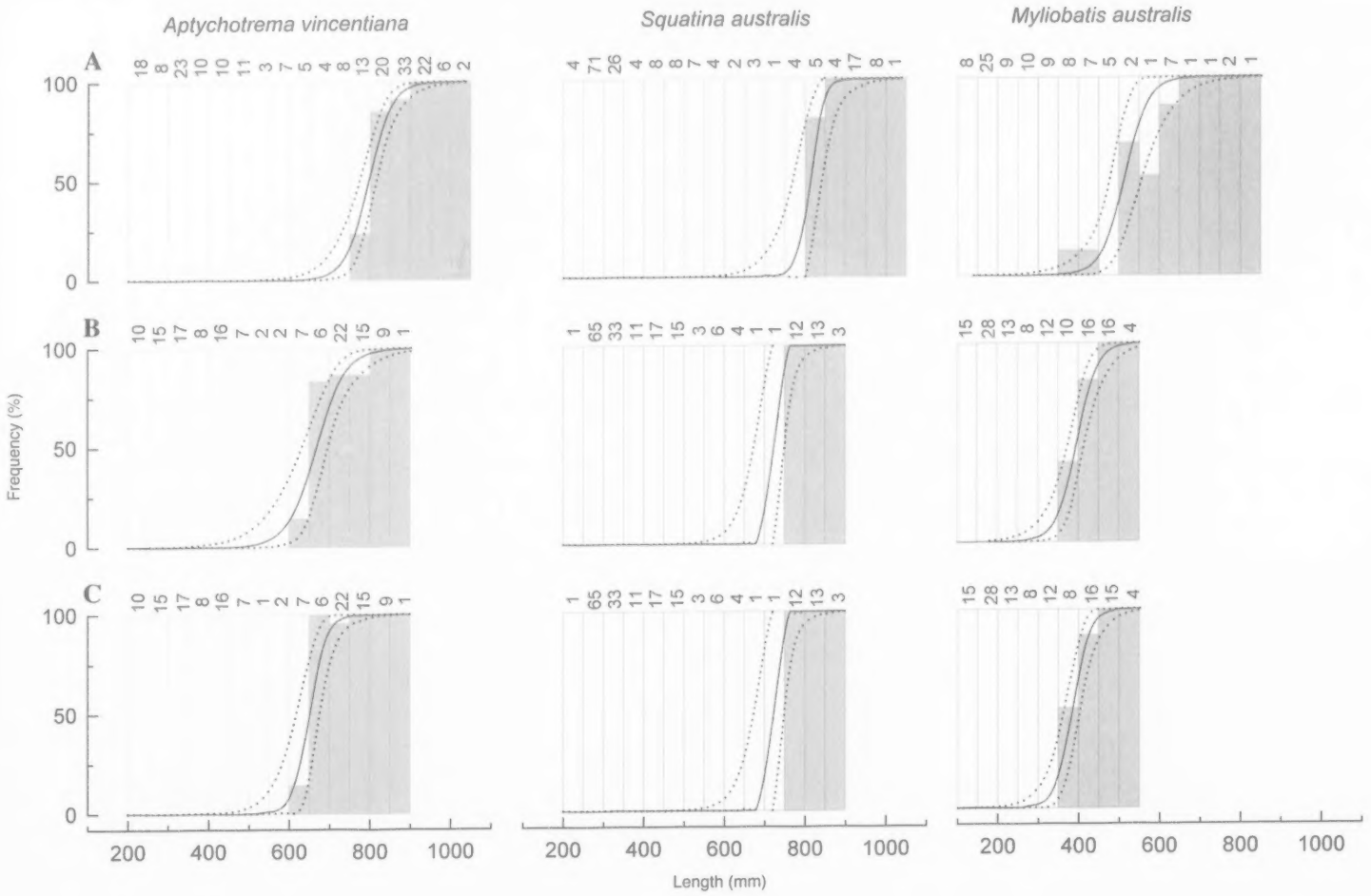

Figure 5

Percent frequencies of occurrence, including samples sizes, of mature *Aptychotrema vincentiana*, *Squatina australis*, and *Myliobatis australis* in sequential 50-mm length classes (gray bars) for (**A**) females and (**B**) males by using gonadal criteria as the indicator of maturity, and for (**C**) males by using full clasper calcification as the criterion. The logistic curve (solid line) and its 95% confidence limits (dotted lines) for each species show the probability that an individual is mature in relation to its total length. Sample sizes are shown above the histograms for each of the 50-mm length classes. Length refers to total length (*TL*), except in the case of *M. australis* where it refers to disc length (*DL*).

Compositions of the catches taken by the three fishing methods

Our results indicate that the elasmobranch component of the catches taken by demersal trawlers on the lower west coast of Australia is dominated by rays, which comprise 10 of the 14 elasmobranch species caught by this method. Furthermore, these batoids were either small species, e.g., stingarees, or represented by smaller individuals, e.g., *Aptychotrema vincentiana* and *M. australis*. Indeed, the four small species of stingaree (Urolophidae) caught by trawling contributed as much as two-thirds to the total trawl catch of elasmobranchs and were so abundant in samples collected during an extensive trawling study along the lower west coast of Australia that they collectively contributed 17.5% to the total biomass of the 172 fish species caught during that study (Hyndes et al., 1999). The large number of small batoids caught paralleled the situation recorded for other trawl fisheries, including the multispecies bottom trawl fishery off Argentina (Tamini et al., 2006). As with the large ray species, the only two shark species taken in appreciable numbers in our study, *H. portusjacksoni* and *S. australis*, were represented predominantly by small individuals.

The large number of elasmobranchs taken by prawn and scallop trawling emphasizes the lack of selectivity of this fishing method for its targeted species. Indeed, Bonfil[2] has stated that towed nets are the most indiscriminant of all fishing gears because they are designed to capture everything in their path and thus inevitably encounter a large number of nontarget species. The susceptibility of small demersal elasmobranchs to capture by trawling is due to their limited mobility and benthic lifestyle (see also Stobutzki et al., 2001, 2002; Walker, 2005a; Tamini et al., 2006) and to the trawlers often operating in nearshore waters, which typically act as nursery areas for several elasmobranch species, including *H. portusjacksoni* (White and Potter, 2004; Jones et al., 2008; Kinney and Simpfendorfer, 2009). The catches of elasmobranchs taken by trawls in our study comprised only six individuals that were retained as byproduct compared with the 2980 individuals discarded as bycatch.

Although the three species targeted by gillnetting, *C. obscurus*, *M. antarcticus*, and *Furgaleus macki*, collectively accounted for just over half of the total number of elasmobranchs caught by this method, the contribution of all retained species (i.e. including byproduct), accounted for three quarters of the total. This is very similar to the situation recorded for a gillnet fishery in southeastern Australia (Walker et al., 2005). The remainder of the catch (i.e., the bycatch) was still substantial, however, emphasizing that a considerable number of the sharks and rays caught by gillnet were discarded, as has been reported in gillnet fisheries elsewhere in the world (e.g., Perez and Warhlich, 2005).

The mesh sizes of the gillnets (165 and 178 mm) were selected to catch the three targeted species, *C. obscurus*, *M. antarcticus*, and *F. macki*, at a marketable size which, depending on the species, typically corresponded to modal fork lengths of between 800 and 1200 mm (McAuley and Simpfendorfer, 2003). This mesh selectivity accounts for the fact that the *TL* of the majority of *A. vincentiana* and *S. australis* in our gillnet catches fell within a relatively narrow range of 700–1000 mm, with the latter length closely approximating the maximum length recorded for these two species during the present study (Table 5). However, the *TL* for *H. portusjacksoni*, the second most abundant species in the gillnet catches, spanned the full range of this species in southwestern Australian waters (Jones et al., 2008). The capture by gillnet of a substantial number of *H. portusjacksoni* with lengths less than 700 mm is attributable to the tendency for all sizes of *H. portusjacksoni* to become entangled in gillnets as a result of their possessing prominent dorsal fin spines (Walker, 2005a). In the case of the ray *M. australis*, the larger individuals were proportionately less in gillnet than longline catches because this wide disc-shaped species becomes increasingly deflected from the net as it grows larger (Walker, 2005a).

Longlining was so successful at targeting *M. antarcticus* that this shark contributed nearly two thirds to the total elasmobranch catch taken by this method and, together with the other two targeted species, *C. obscurus* and *F. macki*, represented nearly 70% of that total catch. However, those last two species were not abundant in these catches. In fact, the second to fifth most abundant species were bycatch species. Although 11 of the 19 nontargeted elasmobranch species were typically retained as byproduct, none of those species was numerous and collectively accounted for only ~7% of the elasmobranch catch. From the above, it follows that the contribution of bycatch to the longline catches (~26%) was similar to that in the gillnet catches. However, unlike the situation with gillnetting, the bycatch species *S. australis* was never caught on longline hooks, presumably because this squatinid is an ambush predator that targets mobile prey such as teleosts and cephalopods (E. Sommerville, personal commun.[3]).

Although the use of nMDS ordination and associated tests emphasized that the species compositions of the elasmobranchs caught by trawling, gillnetting, and longlining differed markedly, SIMPER showed that *H. portusjacksoni* was a major typifying species for the elasmobranchs taken by trawling in relatively shallow waters and by gillnetting and longlining in deeper and more offshore waters. This bycatch species is thus clearly abundant and widely distributed throughout the inshore and more offshore coastal waters of southwest-

[2] Bonfil, R. 2000. The problem of incidental catches of sharks and rays, its likely consequences, and some possible solutions. *Shark Conference 2000 online documents*, 8 p. (Pacific Fisheries Coalition, http://www.pacfish.org/sharkcon/documents/bonfil.html, accessed May 2010).

[3] Sommerville, Emma. 2007. Centre for Fish and Fisheries Research, Murdoch Univ., Murdoch, Western Australia, 6150.

ern Australia. The finding that the ray *D. brevicaudata* was the most important typifying species in the longline samples indicates that this bycatch species was consistently present in reasonable numbers in water depths of approximately 70 m. Although the total number of *M. antarcticus* obtained by longlining was far greater than that of *D. brevicaudata*, *M. antarcticus* was occasionally taken in large numbers and, at other times, not caught at all, reflecting the tendency for this shark species to school (Lenanton et al., 1990; Last and Stevens, 2009).

Length compositions, sex ratios, and habitats of the four selected bycatch species

Our data indicate that the maximum lengths of the females of *H. portusjacksoni*, *A. vincentiana*, *S. australis*, and *M. australis* exceed those of males by 37%, 13%, 14%, and 31%, respectively. Moreover, for each species, the sex ratio did not differ significantly from parity among their juveniles, and the females dominated the length classes of the larger individuals. The resultant trend for the overall sex ratios for *H. portusjacksoni* and *A. vincentiana* to significantly favor females indicates that the females of at least these two species live longer than their males. Such a conclusion for *H. portusjacksoni* in southwestern Australian waters is consistent with the results of Tovar-Ávila et al. (2009), who showed that, in southeastern Australia, the maximum age of the females (35 years) of this species is greater than that of males (28 years). Although the overall sex ratios of *S. australis* and *M. australis* did not differ from parity, those ratios were almost certainly attributable to the larger individuals of these two species being proportionately less well represented in the overall samples of those species. In the case of *S. australis*, the capture of fewer larger individuals was mainly due to this species not being taken by longlining fisheries in deeper, offshore waters, where they had been caught by gillnetting, and thus the overall samples were swamped by juveniles caught by trawls in their nursery areas. The conclusion that larger females were under-represented in the overall catch of *M. australis* is consistent with a tendency for the larger individuals, which would presumably have been predominantly females, to be deflected from the net.

The difference between the maximum lengths of the females and males of *H. portusjacksoni* in southwestern Australian waters (37%) was far greater than the 19% and 10% differences recorded for two populations of this species in southeastern Australian (Tovar-Ávila et al., 2007) and the 15% difference found farther north in eastern Australia (Powter and Gladstone, 2008). The trend for females to attain a larger size than that of males parallels that reported by Cortés (2000) for populations representing 164 species and 19 families of sharks. However, the average difference between the sizes of females and males reported by Cortés (2000) was 10% and thus smaller than the differences observed for particularly *H. portusjacksoni* and *M. australis*.

Comparisons of the length-frequency distributions for each of *H. portusjacksoni*, *A. vincentiana*, *S. australis*, and *M. australis* in samples obtained from trawling in inshore waters, and by gillnetting and longlining farther offshore, indicated that all four species use shallow, inshore waters as nursery areas and that substantial numbers of the adults of *S. australis* and *M. australis* are also present in these inshore habitats. The tendency for *M. australis* to use inshore areas as nursery areas in southwestern Australia is emphasized by the considerable numbers of juveniles of this species that were caught during a study of a permanently open estuary on the south coast of Western Australia (Potter and Hyndes, 1994). Furthermore, the juveniles of *H. portusjacksoni* are also abundant in inshore waters off eastern Australia (McLaughlin and O'Gower, 1971). Because several of the mature females of *A. vincentiana* caught in inshore waters contained full-term embryos, they would have been poised to give birth in those waters. However, because adults of *H. portusjacksoni*, *A. vincentiana*, and *M. australis* were caught by gillnetting and longlining, and *S. australis* was caught by longlining, some individuals of each of these species move offshore as they increase in size and some may even live permanently in offshore waters.

Lengths at maturity and their implications

The greater maximum length attained by females than by males of each of the four elasmobranch species was accompanied, on the basis of gonadal criteria, by a greater L_{50} at maturity, and the differences in L_{50} ranged from 12% for *S. australis* and 19% for *A. vincentiana* to as high as 28% for *M. australis* and 36% for *H. portusjacksoni*. The trend for the females of these species to mature at a larger size than that of males follows the overall trend exhibited by shark species (Cortés, 2000).

The values derived for the L_{50} at maturity for the males of *A. vincentiana*, *S. australis*, and *M. australis* by using full clasper calcification as the criterion for maturity did not differ significantly from the corresponding values derived by using gonadal maturity as that criterion. This result parallels that recorded for *H. portusjacksoni* by Jones et al. (2008), for *Squalus megalops* by Braccini et al. (2006), and for *Trygonorrhina dumerilii* by Marshall et al. (2007). Thus, to obtain data that can subsequently be used to derive a reasonable proxy for the L_{50} for males at maturity, scientists can rapidly record the lengths of males, determine whether or not their claspers are calcified, and then immediately return them live to the sea. Furthermore, for each of the four species, all of the males with uncalcified claspers and most of those with partially calcified claspers possessed immature (stage 1 or 2) gonads, whereas those with fully calcified claspers almost invariably contained mature (stage 3 or 4) gonads and this finding thus accounts for the L_{50} at maturity not being significantly different when gonadal and clasper calcification criteria are used.

On the basis of our calculations of the L_{50} at maturity for females and males of each of the four selected bycatch species, the overall percentages, in trawl samples, of *H. portusjacksoni*, *S. australis*, and *M. australis*, whose individuals would not typically have had the potential to reproduce, were particularly high, with values ranging from 90% to 97%. These high values are attributable to trawling taking place mainly in shallow inshore waters that typically act as nursery areas. The importance of protecting the newborn and young juveniles of species that have well-defined nursery areas has been emphasized by Walker (2005a). The far lower percentage of *A. vincentiana* with lengths less than the L_{50} at maturity in trawl samples than was the case with the other three species is attributable to the tendency for this species to occupy inshore waters throughout its life.

The smaller proportion of individuals of *H. portusjacksoni*, *A. vincentiana*, *S. australis*, and *M. australis* with lengths less than their L_{50} at maturity in gillnet than in trawl catches reflects a combination of the following: 1) differences in gear selectivity; the mesh sizes of gillnets are chosen with the purpose of catching targeted species at a sufficient size to be commercially marketed (Simpfendorfer and Unsworth, 1998; McAuley and Simpfendorfer, 2003) and thereby obtaining proportionately more of the larger, mature individuals of these four bycatch species than their juveniles; and 2) the location of gillnetting in deeper, offshore waters and thus beyond typical nursery areas.

Mortality

Onboard sampling of the catches obtained by the three fishing methods during commercial operations was made difficult by the small size of the fishing boats and the rapidity with which the fishermen worked to retrieve the retained species and discard the bycatch. It was thus not possible to determine precisely the fishing-induced mortality of the individuals of each bycatch species taken by each fishing method and, in particular, the mortality of *H. portusjacksoni*, *A. vincentiana*, *S. australis*, and *M. australis*. From our observations, however, it is apparent that, in the case of trawling, many individuals died while in the net and those that survived were often so badly injured during sorting that they would have been unlikely to survive after release. From our observations, we believe that the level of mortality associated with trawling is greater than that suggested by Laurenson et al.[1], who proposed that approximately half of the elasmobranchs taken by trawling during a research project on the lower west coast of Australia was likely to die during capture or after being discarded. Indeed, in a detailed study of the bycatch of Australia's northern prawn trawl fishery, Stobutzki et al. (2002) showed that as much as two-thirds of the sharks and rays caught by this method died while still in the net, and thus the overall mortality, i.e., including individuals that subsequently died from the trauma of capture, would have been higher. It should also be recognized that the pregnant females of the smaller species of rays (White and Potter, 2004) and *S. australis* and *M. australis* tended to abort after capture, thus adding a further detrimental effect to the populations of those species.

It was evident that the individuals of most species, including those of the three targeted species, *M. antarcticus*, *C. obscurus*, and *F. macki*, and several bycatch species, such as *M. australis* and *S. australis*, had died by the time the gillnet was retrieved. It is proposed that this high mortality was related to the very long soak times of the gillnets (up to 24 h), which is consistent with the observation that mortality was far lower in a gillnet study conducted in southeastern Australia in which soak times were only ~8 h (Walker et al., 2005). Furthermore, the long soak times led to the elasmobranchs in the nets becoming infested by sea lice (*Cirolana* sp.) and to attack by leatherjackets (*Monacanthid* spp.), thus hastening the death of species such as *M. australis*. Moreover, although *H. portusjacksoni* frequently survived capture by gillnets, the individuals of this species were often severely injured while being forcibly removed from the gillnets.

In contrast to the situation with gillnetting, the majority of elasmobranchs survived capture by longlining and thus, in general, the individuals of bycatch species caught by hooks were able to be returned to the sea alive. The high survival of elasmobranchs caught by longlining in southwestern Australia is presumably attributable, at least in part, to the short set times (~3 h) for this fishing method.

Implications for ecosystem-based fisheries management

Traditional fisheries management has focused on ensuring that the populations of targeted species are maintained at levels that are considered sustainable. However, fisheries regulations aimed at constraining the exploitation of targeted species may provide little protection for bycatch species, and thus commercial fisheries can have an equal or even greater impact on the populations of bycatch species. In contrast, ecosystem-based fisheries management, i.e., an ecosystem approach to fisheries, requires that the populations of bycatch species in an ecosystem, as well as those of the targeted and byproduct species, are sustained. It is thus relevant that our study revealed that many individuals of the elasmobranch bycatch species caught by commercial fisheries, and particularly by trawling, were immature and, together with our observations and the results of other studies, strongly indicated that mortality is high among these individuals. The problems posed by such fisheries-induced mortalities on these bycatch species are exacerbated because elasmobranchs have low biological productivity and are therefore susceptible to overexploitation (Stevens et al., 2000; Walker, 2005a). Thus, while it is recognized that the trawl, gillnet, and longline fisheries of southwestern Australia are not large, the removal of even moderate numbers from the population of any elasmobranch species has the potential to affect that population at a local level (Walker, 2005a).

In the context of the ecosystem-based fisheries management framework, every attempt should be made to reduce, where practical, the amount of bycatch. In view of the high mortality of the bycatch species taken by trawlers and gillnetters, commercial fishermen should be encouraged to explore ways of reducing the amount of bycatch and of increasing survival among discarded individuals. Thus, with trawling for example, fishermen could explore the effectiveness of bycatch reduction devices, reduce the duration of trawls and onboard handling time, and unload the catch into water tanks before sorting. In the case of gillnetting, fishermen could explore whether a reduction in the soak time of their nets leads to a decrease in the mortality of the bycatch and an increase in the market quality and thus the value of the flesh of the retained species.

The biological and catch data produced during this and other studies on locally abundant bycatch species of elasmobranchs (White et al., 2001; 2002; White and Potter, 2005; Marshall et al., 2007) indicate that trawl, gillnet, and longline fisheries may be having a direct impact on the populations of these species in southwestern Australia. The acquisition of these data now enables managers to determine whether the impacts of commercial fisheries on the populations of bycatch species justify modifying fishing regulations to ensure that the risks to the sustainability of these species are reduced and that the integrity of the ecosystem is thus maintained. Such risks could readily be achieved through the use of rapid assessment techniques, such as those described by Stobutzki (2001; 2002) and Walker et al. (2005).

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Ontogenetic patterns and temperature-dependent growth rates in early life stages of Pacific cod (*Gadus macrocephalus*)

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Abstract—Pacific cod (*Gadus macrocephalus*) is an important component of fisheries and food webs in the North Pacific Ocean and Bering Sea. However, vital rates of early life stages of this species have yet to be described in detail. We determined the thermal sensitivity of growth rates of embryos, preflexion and postflexion larvae, and postsettlement juveniles. Growth rates (length and mass) at each ontogenetic stage were measured in three replicate tanks at four to five temperatures. Nonlinear regression was used to obtain parameters for independent stage-specific growth functions and a unified size- and temperature-dependent growth function. Specific growth rates increased with temperature at all stages and generally decreased with increases in body size. However, these analyses revealed a departure from a strict size-based allometry in growth patterns, as reduced growth rates were observed among preflexion larvae: the reduction in specific growth rate between embryos and free-swimming larvae was greater than expected based on body size differences. Growth reductions in the preflexion larvae appear to be associated with increased metabolic rates and the transition from endogenous to exogenous feeding. In future studies, experiments should be integrated across life transitions to more clearly define intrinsic ontogenetic and size-dependent growth patterns because these are critical for evaluations of spatial and temporal variation in habitat quality.

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Fluctuations in the distribution and abundance of marine species are highly influenced by climate-driven changes in ocean conditions (Perry et al., 2005). In the Gulf of Alaska and Bering Sea, oceanographic regimes linked to climate conditions (Hollowed et al., 2001; Peterson and Schwing, 2003) occur across a variety of time scales, from seasonal to multidecadal (Hunt and Stabeno, 2002). These climate cycles have been linked to major shifts in the composition of valuable groundfish communities (Anderson and Piatt, 1999). Imposed upon this variation is the potential for longer-term climate changes, such as the warming of surface waters and loss of sea ice (e.g., Hunt et al., 2002). Such warming trends have already been observed in the Gulf of Alaska (Royer and Grosch, 2006) and Bering Sea (Stabeno et al., 2007). The response of individual populations and entire communities to environmental forcing depends upon the physiological and behavioral traits of individual species and the cumulative set of trophic interactions between species (Freitas et al., 2007; Yatsu et al., 2008; Hurst et al., 2010).

Spatial and temporal variation in temperature and prey availability are considered to be primary drivers of growth and survival in early life stages of fishes and their influence on recruitment has been central to various generalized models of recruitment (see review by Cowen and Shaw, 2002). The oscillating control hypothesis (OCH) states that population production of groundfish in the Bering Sea is linked to climate-driven patterns of prey production: cold winters with extensive sea ice result in early, low-density blooms in cold water, resulting in reduced survival of larvae (Hunt and Stabeno, 2002). Evaluation of the OCH and predicting potential responses to future aspects of climate change require detailed information on the temperature-dependent vital rates of early life stages of fish (Kristiansen et al., 2007; Hollowed et al., 2009; Rijnsdorp et al., 2009).

Pacific cod (*Gadus macrocephalus*) is a widespread marine species on continental shelves throughout the eastern and western North Pacific and Bering Sea. They are an important component of North Pacific and Bering Sea fisheries and food webs. In recent years, U.S. landings of Pacific cod trail only those of Alaska walleye pollock (*Theragra chalcogramma*) and Atlantic and gulf menhaden (*Brevoortia tyrannus* and *B. patronus*) (NMFS, 2008). Between 2002 and 2006, U.S. landings of Pa-

Table 1

Summary of experiments conducted at the Alaska Fisheries Science Center laboratory in Newport, Oregon, where growth rates were determined for early life stages of Pacific cod (*Gadus macrocephalus*) collected from the central Gulf of Alaska.

Stage	Temperatures (°C)	Year	Experiment duration (dah=days after hatching)	Sample type	No of tanks	*n* fish
Eggs	0, 2, 4, 6, 8	2006	Fertilization to hatching	Measured at hatching	15	30/sample
Preflexion larvae	3, 8	2007	Hatching to 35 dah	Tank sample	6	10/sample
	2, 5, 8	2008	Hatching to 36 dah	Tank sample	9	10/sample
Postflexion larvae	2, 4, 8, 11	2007	50 to 105 dah	Tank sample	12	10/sample
Juveniles	2, 5, 8, 11	2008	approx. 132 to 150 dah	Serial measures	12	10/tank

cific cod averaged 28 times those of Atlantic cod (*Gadus morhua*).

Despite the pervasive influence of temperature on all aspects of biology and its potential linkage to recruitment patterns, there has been little examination of the thermal ecology of Pacific cod. The effects of temperature on the vertical distribution of larvae (Hurst et al., 2009) and juveniles (Davis and Ottmar, 2009) have been examined. Thermal effects on growth of Pacific cod has been examined in only the very early life stages: development rates of eggs and prefeeding larvae (Alderdice and Forrester, 1971; Laurel et al., 2008) have been examined across a wide range of temperatures. In addition, B. J. Laurel (unpubl. data) compared the effects of prey density on growth of preflexion larvae at two temperatures. However, these studies are insufficient to describe the functional response to temperature for larvae, and as of yet, no data exist for later larval stages or juveniles.

In this article we describe the growth of early life stages of Pacific cod as a function of temperature and body size. Separate experiments were conducted with preflexion larvae, postflexion larvae, and postsettlement juveniles. From these experiments and published data on embryos, we determined the parameters for models of stage-specific growth and for an integrated model of size- and temperature-dependent growth. These functions will be used to evaluate the relative contributions of temperature and feeding conditions to observed variation in growth among wild Pacific cod (Folkvord, 2005; Hurst et al., 2010).

Materials and methods

We determined the thermal sensitivity of growth rates at three life stages: preflexion larvae, post-flexion larvae, and postsettlement juveniles (Table 1). Growth rates at each ontogenetic stage were measured in three replicate tanks at four to five temperatures, encompassing the range likely to be encountered by fish in the Gulf of Alaska and Bering Sea. Nonlinear regression was used to describe the relationship between growth rate and temperature at each developmental stage and to describe the combined effects of temperature and body size on growth rates of early life stages.

Preflexion larvae

Two experiments were conducted to describe the growth of Pacific cod larvae after hatching. In 2008, fish were reared at 2°, 5°, and 8°C to 36 days after hatching (dah). These data were combined with data on fish reared under identical conditions to 35 dah at 3°C and 8°C in 2007 (B. J. Laurel, unpubl. data). The 8°C treatment was conducted in both experiments to evaluate potential differences in overall growth rates between years.

Fish for the larval growth experiments were reared in the laboratory from eggs collected from spawning adults. Female and male Pacific cod were caught by commercial jigging gear from spawning grounds in Chiniak Bay, Kodiak Island, Alaska. The gametes were mixed and placed into 4-L incubation trays at 4°C. At 24 hours after fertilization, fertilized eggs were shipped in insulated containers to the Alaska Fisheries Science Center's (AFSC) laboratory facilities in Newport, Oregon. Eggs were transferred to flow-through 4-L plastic trays and incubated at 4°C. Hatching occurred 19–22 days after fertilization, after which larvae were transferred to larval rearing tanks.

Experimental rearing tanks were 100-L cylinders with conical bottoms and dark green walls. Water was supplied to the tanks at a rate of 250 mL/min. Weak upwelling circulation was maintained in the tank by positioning the in-flow at the bottom center of the tank and with light aeration. Light regime during larval rearing was maintained at 12:12 h light:dark; light was provided by overhead fluorescent bulbs at a level of 6.7 $\mu E/m^2s$ at the water surface.

Larval growth experiments were initiated by stocking rearing tanks (maintained at the egg incubation temperature of 4°C) with 400 larvae which hatched over a 4-day period in the middle of the hatch cycle. The last day that newly hatched fish were stocked into rearing tanks is nominally referred to as experimental day 0. After the tanks were stocked with fish, tank temperatures were adjusted to treatment temperatures over 2 days. Larvae were reared on a combination of rotifers

(*Brachionus plicatilis*) enriched with Algamac 2000 (Aquafauna, Hawthorne, CA; Park et al., 2006) and microparticulate dry food (Otohime A, Marubeni Nisshin Feed Co., Tokyo). Rotifers were supplied at densities of 4 prey/mL twice daily and dry food was provided 2–3 times per day.

At periodic intervals, a subsample of 10 larvae was removed from each tank to determine the mean size of larvae in the tank. For the 2007 experiments, six samples were drawn at 7-d intervals (starting on day 0). For the 2008 experiments, all tanks were sampled on days 0, 10, 23, and 36. Sampled larvae were individually photographed under magnification and measured from calibrated digital photographs using ImagePro® (Media Cybernetics, Bethesda, MD) software. The morphometrics used in these analyses were standard length (L_S) and body depth of the myotome at the anus (D).

Dry weight of individual larvae was calculated using a two-step model with L_S and D developed from an independent collection of similar size Pacific cod larvae reared in the laboratory under identical conditions. These fish were individually photographed and dried on preweighed foil at 68°C for at least 24 hours before determination of dry mass (to 1.0 μg) with a microbalance. Fourty-four fish with L_S of 5 to 11 mm were sampled periodically over the first 45 dah. First, the body depth deviation (D_{Dev}) was calculated for each fish, reflecting variance in "condition" from the equation

$$D_{Dev} = D - 0.0873 \cdot e^{0.2164 \cdot L_S}. \quad (1)$$

Individual dry mass (M_D mg) was calculated from D_{Dev} and L_S from the equation

$$M_D = 0.0204 \cdot e^{0.3734 \cdot L_S} + (0.9685 \cdot D_{Dev} - 0.1113). \quad (2)$$

These equations explained 97.8% of the variation in dry mass of fish in the sample.

Growth rates were calculated for each replicate tank from the increase in mean size of fish in measured subsamples. Growth in length (g_L, mm/d) and mass (g_M, /d) were calculated from linear regression of mean length and ln-transformed mass against sampling date.

Postflexion larvae

Growth rates of postflexion larvae were measured in a separate experiment applying similar procedures. Experiments were established with fish 50 dah, reared at 8°C under conditions similar to those described above for preflexion larval experiments. Given the variation in body size among cultured fish, each fish was assigned to one of three size categories on the basis of visual estimation. This sorting by size was done to minimize the potential for intracohort cannibalism frequently observed in larval and juvenile gadids (Folkvord and Otterå, 1993, Sogard and Olla, 1994). One group of 35–40 larvae from each size category was assigned to each temperature treatment (2°, 4°, 8°, 11°C). In addition, a sample of 15–20 fish from each size category was sacrificed to determine initial size distributions.

After establishment of experimental groups (day 0), temperatures were adjusted to target temperatures at a rate of 2°C per day. Larvae were offered particulate food three to four times per day, supplemented with enriched rotifers twice per day (first 20 d only). As fish grew, larger size particulate food (up to 620 μm) was included in daily feedings. A subsample (7–10 fish) was drawn from the 8°C and 11°C treatments on day 18 and from the 2°C and 4°C treatments on day 24. The experiments were ended and all surviving larvae were measured on day 32 for the 8°C and 11°C treatments and on day 45 for the 2°C and 4°C treatments. Lengths (L_S and L_T) of all sampled larvae were measured with digital calipers under a dissecting microscope and wet masses (M_W) were measured with a microbalance. Dry mass (M_D) of each larvae was determined after 48 hours in a drying oven at 50°C.

Growth rates were calculated from the increase in mean size of fish in measured subsamples. Growth in length (g_L, mm/d) and mass (g_M, /d) were calculated from linear regression of mean length and ln-transformed mass against sampling date.

Postsettlement juveniles

Age-0 Pacific cod were captured from Kodiak Island juvenile nurseries in July 2008 with a 36-m beach seine. Fish were maintained for at least 48 hours at the AFSC Kodiak Laboratory in ambient seawater before shipment to the AFSC's laboratory in Newport, Oregon. Fish were shipped overnight in insulated containers filled with seawater and oxygen. Before use in laboratory experiments, fish were maintained in 1-m diameter round tanks with flow-through seawater maintained at 8–10°C. Fish were fed thawed krill and commercially available pellets on alternating days.

The experiment was initiated by assigning fish-size categories based on visual estimation and stocking fish into experimental tanks. One tank of each size category (n=3) was assigned to each temperature treatment (n=4; 12 tanks total). After establishment of experimental groups, temperatures were adjusted to treatment temperatures (2°, 5°, 8°, and 11°C) and fish were acclimated to the treatment temperature for 10 days.

Experimental tanks were 66×45.7 cm, filled to a depth of 23.2 cm. During the experiment fish were fed thawed krill to apparent satiation once per day. In addition, a gelatinized combination of squid, krill, herring, commercial fish food, amino acid supplements, and vitamins was provided three times per week. Lights were maintained on a 12:12 h light:dark photoperiod for all experiments. Tanks were checked twice daily for mortalities, and dead fish were removed, weighed, and measured.

Growth rates were estimated by measuring (L_T to 1 mm) all fish in the experiment three times at 10-d intervals. To minimize stress to small fish from repeated handling, wet masses were measured only at the end

of the experiment. Wet mass (M_W) of individual fish at earlier sampling points was estimated from regressions based on measurements of fish collected but not used in this experiment and the final experimental measurements.

Growth rates (g_L and g_M) of juvenile cod were determined by regression of the measurements of fish length and ln-transformed mass against sampling date. In lieu of marking the 7–10 individual fish in each tank, we assumed that size rank was maintained within each replicate tank during the experiment. Fish that died during the experiment were not included in statistical analyses.

Growth models

For each of the life stages examined (egg–embryos, preflexion larvae, postflexion larvae, juveniles), temperature-dependent growth functions were estimated for growth in length and mass. For consistency with the most commonly applied field measures of body size, growth rates of embryos and larvae were expressed in terms of L_S and M_D, and juvenile growth rates as L_T and M_W. Growth of postflexion larvae were expressed in both sets of measures.

For each life stage, a second-order polynomial function was fitted to describe the relationship between temperature and growth rate. For consistency in best-fit models, the second-order term was maintained, although it was not statistically significant in some cases. For these models, mean temperatures measured during the growth interval were applied, rather than experimental target temperatures. The mean growth rate measured in each replicate tank (n=3 per temperature) was used as the level of observation.

In addition to stage-specific models, an integrated model of size- and temperature-dependent growth (STDG) was developed (Folkvord, 2005). Data for the model were derived from the above experiments on larvae and juveniles and from previously published data on the hatching times and sizes as a function of temperature (Laurel et al., 2008). Despite representing easily identified discrete life stages with differing habitats, data on growth of embryos before hatching were included with posthatch data to clarify intrinsic patterns in potential growth rates through the early life stages. Growth rates of prehatch embryos were estimated from the size and age (days after fertilization) at hatching, assuming $M_{D=}$0.01 μg and $L_{S=}$0.0 mm at fertilization. In order to standardize measures across life stages, measured M_W for juveniles was converted to M_D and measured L_T was converted to L_S on the basis of measurements of similarly size fish (Hurst, unpubl. data).

The integrated STDG model was initially fitted with generalized additive models (GAM) to examine the potential effects of nonlinear interactions between mass and temperature on growth. These nonlinear, nonparametric regression techniques do not require *a priori* assumptions on the shape of the relationship between the dependent and independent variables. After evaluation of potential interactions based on evaluation of the generalized cross validation (GCV), a parametric model formulation was selected that best represented patterns in the growth data. Final models were fitted with parametric nonlinear regression in Statistica (vers. 6.0, StatSoft, Tulsa, OK). This approach was undertaken separately to provide STDG models for growth expressed in mass (M_D) and length (L_S).

Results

Preflexion larvae

Mean size of larvae at hatch was slightly larger in the 2007 experiment than in the 2008 experiment (L_S 5.16 vs. 4.90 mm; $F_{[1,60]}$=45.4, P<0.001). However, there was no significant difference among years in growth rates of preflexion larvae reared at 8°C (g_L $F_{[1,4]}$=1.52, P=0.237; g_M $F_{[1,4]}$=3.90, P=0.119), therefore data from the two experiments were combined to describe the effect of temperature on growth rate. In addition, there were no differences in growth rates among replicate tanks at a given temperature (tested as the interaction between day and tank on mean size, all P>0.05).

Growth in length and mass of Pacific cod larvae was significantly affected by rearing temperatures across the range examined (Fig. 1; g_M $F_{[3,11]}$=30.0, P<0.001; g_L ($F_{[3,11]}$=59.4, P<0.001). After 35 days, fish reared at 8°C were 2.6 times larger than fish reared at 2°C (M_D 0.271 vs. 0.104 mg). Growth rates were fitted as a second-order function of temperature (Table 2).

Postflexion larvae

The sorting of fish by size before the establishment of experimental groups produced significant differences in initial sizes of experimental fish (group mean L_S 14.02 to 16.10 mm; P=0.004). Differences among size groups within temperature treatment were generally maintained throughout the experiment but growth rates were slightly higher in the small-size groups than the in large-size groups. The effect of size group was significant for growth expressed as g_M ($F_{[2,6]}$=15.7, P=0.004) but not for g_L ($F_{[2,6]}$=1.78, P=0.248).

Growth in length and mass of postflexion Pacific cod larvae was significantly affected by rearing temperatures across the range examined (Fig. 2; g_M $F_{[3,6]}$=34.3, P<0.001; g_L ($F_{[3,6]}$=63.0, P<0.001). Growth rates (for g_M and g_L) at 11°C averaged 2.2 and 3.0 times, respectively those observed at 3°C in similar size treatments. Growth rates were described as a second-order function of temperature (Table 2).

Juveniles

Sorting of fish by size before the experiment resulted in significant differences in initial size among replicates within temperature treatments (L_T $F_{[8,83]}$=9.46,

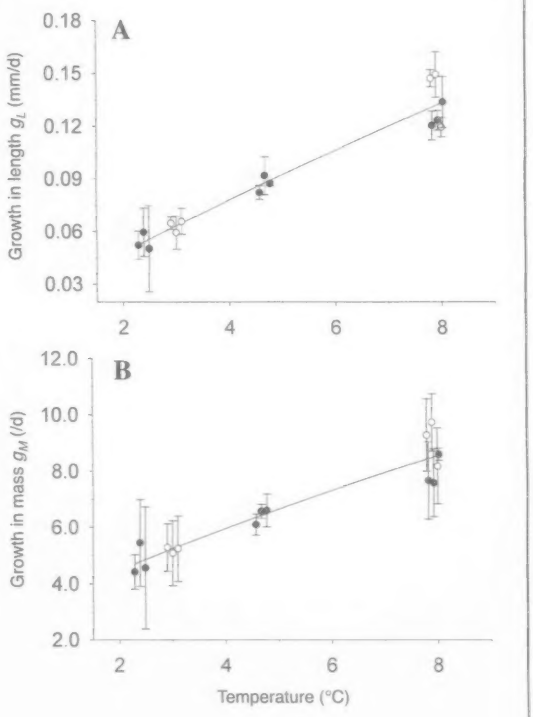

Figure 1

Temperature-dependent growth rates of preflexion larval Pacific cod (*Gadus macrocephalus*) in (**A**) standard length and (**B**) dry mass. Fish used in experiments were the offspring of spawning adults collected in the central Gulf of Alaska in April 2007 (open symbols) and 2008 (filled symbols). Values are the mean growth rates (±standard error) for three replicate tanks at four temperatures. Overlapping points are displaced horizontally for clarity.

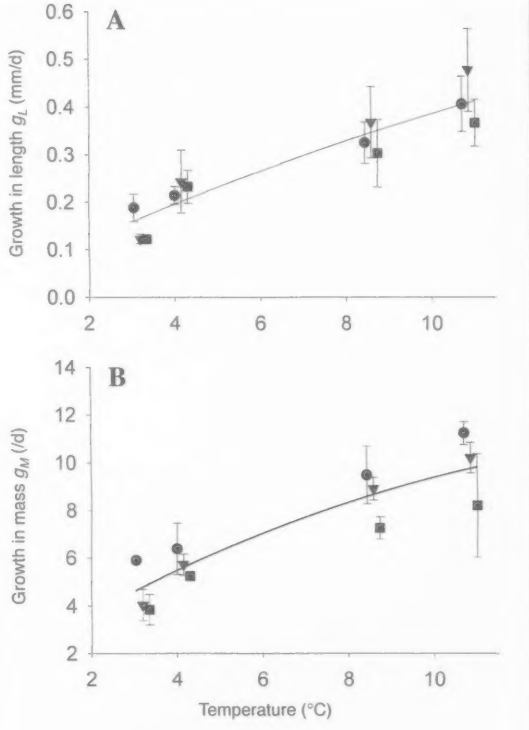

Figure 2

Temperature-dependent growth rates of postflexion larval Pacific cod (*Gadus macrocephalus*) in (**A**) standard length and (**B**) dry mass. Fish used in the experiment were the offspring of spawning adults collected in the central Gulf of Alaska in April 2007. Values are the mean growth rates (±standard error) for three replicate tanks at four temperatures. Symbols represent groups based on initial size sorting of larvae (circle: small; triangle: medium; square: large). Overlapping points are displaced horizontally for clarity.

$P<0.001$). Differential growth during the temperature acclimation period resulted in slight differences in initial sizes among temperature treatments (treatment mean L_T range: 48.8–51.8 mm; $F_{[3,83]}=2.70$, $P=0.051$). Although there were significant differences in growth rates among tanks within temperature treatments, these were not consistent across size groups, resulting in a significant interaction between temperature and size group (g_M $F_{[6,60]}=2.23$, $P=0.052$; g_L: $F_{[6,60]}=2.34$, $P=0.042$).

Growth in length and mass of juvenile Pacific cod was significantly affected by rearing temperatures across the range examined (Fig. 3; g_M $F_{[3,6]}=59.3$, $P<0.001$; g_L ($F_{[3,6]}=26.7$, $P<0.001$). Growth rates at 11°C averaged 2.9 and 3.7 times (g_M and g_L, respectively) greater than those observed at 2°C in similar size treatments. Best-fit functions describing growth as a second-order function of temperature are shown in Table 2.

General growth model

Models of growth rates of early life stages of Pacific cod indicated a discontinuity from strict allometric scaling during the early larval stage. Growth rates of preflexion larvae were lower than predicted based on a purely ontogenetic model incorporating growth-rate data from embryos to settled juveniles. Therefore, two-stage models were developed to describe growth in the egg stage separately from the posthatch, free-swimming stages. Although growth was a function of both temperature and body size, it was effectively modeled as the product of independent functions of temperature and body size. There were no significant interactions in the sense that the parameters of the temperature-dependence function were not themselves a function of body size. Therefore, embryonic and free-swimming stages shared a single

Table 2

Stage-specific growth models for early life stages of Gulf of Alaska Pacific cod (*Gadus macrocephalus*). Models describe growth in mass (g_M) and length (g_L) as a function of temperature (T) for each stage. r^2 is the coefficient of determination.

Stage		Growth functions	r^2
Eggs–embryos	temperature range: 0–8°C		
	dry weight (μg)	$g_M=3.807+1.493\cdot T-0.032\cdot T^2$	0.929
	standard length (mm)	$g_L=0.104+0.024\cdot T-0.00002\cdot T^2$	0.939
Preflexion larvae	temperature range: 2–11°C		
	dry weight (μg)	$g_M=2.990+0.772\cdot T-0.077\cdot T^2$	0.897
	standard length (mm)	$g_L=0.179+0.015\cdot T-0.0001\cdot T^2$	0.941
Postflexion larvae	temperature range: 3–11°C		
	dry weight (g)	$g_M=1.652+1.059\cdot T-0.028\cdot T^2$	0.830
	wet weight (g)	$g_M=0.531+0.857\cdot T-0.024\cdot T^2$	0.897
	standard length (mm)	$g_L=0.034+0.043\cdot T-0.0008\cdot T^2$	0.882
	total length (mm)	$g_L=0.044+0.019\cdot T-0.001\cdot T^2$	0.889
Juveniles	temperature range: 2–12°C		
	wet weight (g)	$g_M=-0.998+0.579\cdot T-0.022\cdot T^2$	0.826
	total length (mm)	$g_L=-0.081+0.079\cdot T-0.003\cdot T^2$	0.762

temperature-dependence function, differing only in elevation through ontogeny (Fig. 4).

Growth rates of Pacific cod through the early life stages were described by the equations

$$g_L=\begin{cases}0.076+0.029\cdot T-0.00002\cdot T^2 & \text{if stage = embyro}\\ \dfrac{0.076+0.029\cdot T-0.00002\cdot T^2}{1-0.059/e^{L_S^{0.0758}}} & \text{if stage > embryo}\end{cases} \quad (3)$$

and

$$g_M=\begin{cases}(0.454+1.610\cdot T-0.069\cdot T^2)\cdot & \\ e^{-6.725\cdot M_D}+3.705 & \text{if stage = embryo}\\ (0.454+1.610\cdot T-0.069\cdot T^2)\cdot & \\ e^{-6.725\cdot M_D} & \text{if stage > embryo}\end{cases} \quad (4)$$

These equations explained over 88% of the observed variance in growth rates of Pacific cod embryos to post-settlement juveniles (g_M r=0.969; g_L r=0.940). Analysis of residuals from these models indicated greater variance at higher growth rates (small body sizes and higher temperatures), but there were no trends in residuals in relation to experimental temperature or body size that would indicate significant departures from the model.

Discussion

Temperature is the dominant regulator of growth in early life stages of fishes. In this study we examined the ontogenic pattern in growth rate for early life stages of Pacific cod. We demonstrated a deviation from strict allometric scaling, wherein growth rates after hatching are lower than those predicted by body size allometry. We determined parameters for temperature-dependent growth functions in length and mass for specific life stages and for a unified STDG function. These measures of growth potential can be used to evaluate the biotic and abiotic factors regulating the growth and survival of early life stages of Pacific cod in the wild (Folkvord, 2005; Hurst et al., 2010).

Experiments

Because these experiments were conducted across a range of life stages, many aspects of our experimental method had to be adapted for each specific experiment, such as tank volume, prey type, and fish density. However, the most significant differences in method between egg–larval and juvenile experiments were the level of observation and source of fish. To estimate growth rates of embryos and larvae, subsamples of fish were drawn from a large tank population to determine mean size at a specific age (Otterlei et al., 1999; Monk et al., 2008). Change in mean size at age was then used to determine growth rate in each replicate tank. With this approach, there is the potential for size-selective mortality in the experiments to affect estimates of mean growth rates. Such size-selective mortality is most commonly assumed to be the result of predation (including cannibalism in single species culture). However, such an effect is unlikely to have occurred in these experiments: postflexion larvae were sorted by size before growth experiments specifically to avoid potential cannibalism, and we saw no evidence of cannibalism in the experiment (no larvae in samples with fish in their stomachs). Because juvenile fish could be handled, they were measured and returned to the tank and subsequently remeasured, providing

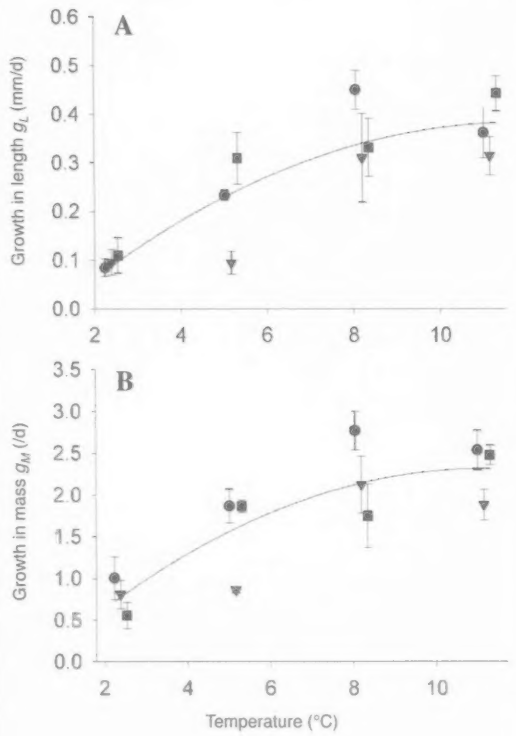

Figure 3

Temperature-dependent growth rates of postsettlement juvenile Pacific cod (*Gadus macrocephalus*) in (**A**) total length and (**B**) wet mass. Fish used in the experiment were collected from nearshore nursery areas at Kodiak Island, Alaska in July 2008. Values are the mean growth rates (± standard error) for three replicate tanks at four temperatures. Symbols represent groups based on initial size sorting of fish (circle: small; triangle: medium; square: large). Overlapping points are displaced horizontally for clarity.

growth trajectories for individual fish. These individual growth rates were then averaged to estimate mean growth rates of fish in each tank (Hurst and Abookire, 2006; Wijekoon et al., 2009).

For experiments with eggs and larvae, we used the offspring of field-caught spawning adults. In each year of experiments, gametes from one or two females were mixed with those of three to five males. Juvenile fish used in experiments were naturally produced and captured after recruitment to juvenile nearshore habitats. Therefore, the genetic diversity among experimental juveniles was significantly greater than that found in experimental eggs and larvae. This difference in potential genetic contributions to growth rates is not expected to have a significant influence on the overall growth patterns described here because maternal and genetic effects on growth have been shown to be small in relation to environmental factors such as temperature (Benoît and Pepin, 1999; Green and McCormick, 2005) and prey availability (Clemmesen et al., 2003).

Ontogenetic patterns of growth

By combining results across life stages, we clarified ontogenetic patterns in growth and length. With the exception of a departure during the preflexion stage, growth patterns followed expected size-dependent allometric patterns throughout much of the early development (Elliott and Hurley, 1995). Growth in mass (g_M) decreased with increases in body size (Wootton, 1990) and growth in length (g_L) was constant across life stages. Although the constancy of g_L across a range of body sizes in early life stages has been noted in other studies (Jones, 2002; Sigourney et al., 2008), those experiments have not generally included the presettlement egg and larval stages incorporated here. Interestingly, in Pacific cod, the general pattern of across-stage similarity in g_L extended from the egg–embryo stage into the juvenile stage.

There was a significant departure from the expected ontogenetic pattern in the preflexion larval period, most clearly observable in the g_L results. Measured g_L among preflexion larvae averaged only 41% of the rates measured for embryos, postflexion larvae, and settled juveniles. Although less readily apparent, a similar departure was observed in mass growth as the decline in g_M between the egg–embryo and preflexion larval stages was greater than expected from allometric patterns accounting for the observed differences in body size. In several studies on the growth of first-feeding gadids, higher growth rates were reported for fish reared on copepods than on cultured rotifers (Conceicao et al., 2010). Unfortunately, technical limitations preclude rearing sufficient quantities of copepods for use in experiments such as ours. For our study, larval Pacific cod were reared on essential-fatty-acid–enriched rotifers, as the best of the practicable prey alternatives. Therefore, it is possible that growth rates of preflexion larvae are under-estimates of maximum potential growth at this stage. However, the effect of prey type is insufficient to completely explain the significantly lower growth rate observed at this stage when compared to other stages. Further, similar observations of reduced growth rates of fishes in the early posthatch phase have been observed in several other studies. Experiments in which growth of haddock (*Melanogrammus aeglefinus*; Martell et al., 2005) was tracked through the egg–larva transition revealed a similar reduction in growth associated with hatching. A similar pattern is apparent in Atlantic cod, but without measurements of embryonic growth rates, the magnitude of decline at hatching could not be determined (Otterlei et al., 1999; Folkvord, 2005). However, these studies document a period of increasing growth rates after hatching, followed by growth rate declines along allometric expectations, indicating a similar overall pattern.

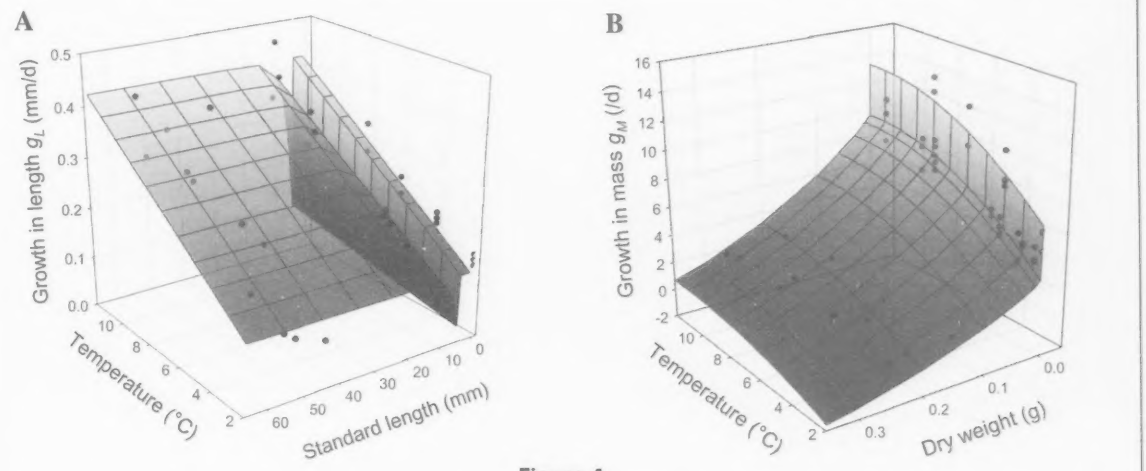

Figure 4

Size- and temperature-dependent growth rates of early life stages of Pacific cod (*Gadus macrocephalus*) from the central Gulf of Alaska in (**A**) standard length and (**B**) dry mass. Points are the tank mean growth rates measured in laboratory experiments. Surfaces are best-fit descriptions of growth rates. Parameter values are presented in Equations 3 and 4.

This reduction in growth during the egg–larva transition appears to be the result of increased metabolic expenditures associated with swimming in posthatch larvae and possibly a reduction in energy available for growth associated with the transition from reliance on endogenous energy stores to exogenous feeding (Torres et al., 1996; Yúfera and Darias, 2007). In Pacific cod, yolk reserves are depleted 3–12 dah, depending on water temperature (Laurel et al., 2008) and stomach fullness increased through the first 28 dah (B. J. Laurel, unpubl. data). The increase in growth rates after the preflexion transitional feeding stage coincides with the onset of diel vertical migrations (Hurst et al., 2009) and increased responsiveness to prey (Colton and Hurst, 2010) among postflexion Pacific cod larvae. The negative departure from an allometrically defined growth pattern after hatching indicates that the first-feeding stage represents a "critical period" in the early life history of Pacific cod and that the consequences for recruitment of this low growth may be greater at low temperatures (Kamler, 1992; Houde, 1996). In addition to inclusion of embryo measurements into larval studies, future studies with other species should encompass other major life history and habitat transitions, such as metamorphosis and settlement in flatfishes (Christensen and Korsgaard, 1999; Neuman et al., 2001) in order to clarify the physiological basis of growth patterns and to determine parameters for growth models.

Based on exploration of model structures for a unified STDG for early life stages of Pacific cod, a two-stage model was developed. The first stage described growth in the egg stage as a direct function of water temperature. The second stage described growth in posthatch fish as a function of water temperature and fish size. In addition to providing the best fit to experimental data, this formulation is logically consistent with the life history. Explicit discrimination between life stages coincides with hatching, whereas the function provides a continuous growth surface for all free-swimming stages. This stage-independent model for posthatch fish provides more realistic growth trajectories in modeling applications where fish are tracked over multiple stages.

Applications of growth models

By quantitatively accounting for the influence of temperature variation, laboratory-determined growth rates are being increasingly used to evaluate factors regulating growth rates of fishes in the wild (Folkvord, 2005; Rakocinski et al., 2006; Hurst et al., 2009). In these analyses, "realized growth" expresses observed growth in the field as a fraction of the potential growth at the encountered field temperatures (Hurst and Abookire, 2006), with field growth rates estimated from changes in mean size, otolith increment measures, or biochemical measures (RNA:DNA). In these studies it is important to recognize that growth rates of individuals are determined by both genetic and environmental factors. Growth models from laboratory experiments generally describe mean growth of a representative population under optimal foraging conditions, which should not be mistaken for the maximum growth rates that would be observed for the fastest growing individual. Therefore, field growth rates should be similarly expressed as a population mean rather than at the individual level. Realized growth rates near 100% indicate that growth rates in the population are directly limited by ambient

temperature variation. In studies of juvenile flatfishes, this temperature regulation of growth has been referred to as the "maximum growth/optimal food condition" hypothesis (Karikiri et al., 1991; van der Veer and Witte, 1993). Conversely, realized growth rates significantly below 100% indicate that growth is regulated by nonthermal environmental factors such as light regime or prey availability (Buckley et al. 2006; Kristiansen et al., 2007; Hurst et al., 2009).

Unfortunately, many studies of growth rates in fishes are conducted over a limited size range and usually within a single life stage. Therefore, these data have limited application where growth rates of wild fish are tracked over longer time periods or through early life history stage transitions. For example, in evaluating the mechanisms responsible for variation in survival and recruitment, it is critical to determine whether growth reductions among wild fish are due to inherent physiologically based patterns (as appears in post-hatch gadids) or are imposed by an unfavorable growth environment (Jones, 2002). In another application of laboratory data to field studies, the back-calculation of hatch dates from estimated temperature-dependent growth rates (Lanksbury et al., 2007) could be biased if ontogenetic patterns in growth variation are not accounted for.

Conclusion

Growth variation in early life stages can result in body-size variation that persists over time and has significant implications for the survival and recruitment of marine fish larvae (Houde, 1996; Jones, 2002). Successful evaluation of the biotic and abiotic factors regulating this underlying variation in growth requires detailed information on the size- and temperature-dependency of potential growth throughout the early life history. Identifying the intrinsic patterns in growth-rate allometry and reductions among preflexion larval Pacific cod was based on the integration of experimental data on embryos and larvae,—stages generally considered in isolation from each other. We suggest that data on embryos be routinely incorporated with larval data to clarify ontogenetic and temperature-dependent growth patterns in the early life history stages of fish.

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Feeding ecology of juvenile Pacific salmon (*Oncorhynchus* spp.) in a northeast Pacific fjord: diet, availability of zooplankton, selectivity for prey, and potential competition for prey resources

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Abstract—We investigated the feeding ecology of juvenile salmon during the critical early life-history stage of transition from shallow to deep marine waters by sampling two stations (190 m and 60 m deep) in a northeast Pacific fjord (Dabob Bay, WA) between May 1985 and October 1987. Four species of Pacific salmon—*Oncorhynchus keta* (chum), *O. tshawytscha* (Chinook), *O. gorbuscha* (pink), and *O. kisutch* (coho)—were examined for stomach contents. Diets of these fishes varied temporally, spatially, and between species, but were dominated by insects, euphausiids, and decapod larvae. Zooplankton assemblages and dry weights differed between stations, and less so between years. Salmon often demonstrated strongly positive or negative selection for specific prey types: copepods were far more abundant in the zooplankton than in the diet, whereas Insecta, Araneae, Cephalapoda, Teleostei, and Ctenophora were more abundant in the diet than in the plankton. Overall diet overlap was highest for Chinook and coho salmon (mean=77.9%)—species that seldom were found together. Chum and Chinook salmon were found together the most frequently, but diet overlap was lower (38.8%) and zooplankton biomass was not correlated with their gut fullness (% body weight). Thus, despite occasional occurrences of significant diet overlap between salmon species, our results indicate that interspecific competition among juvenile salmon does not occur in Dabob Bay.

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Juvenile salmon migrating into coastal waters face a variety of challenges as they adjust to a rapidly changing environment, such as outmigration timing, physiological acclimation, new prey fields, new predators, and competition for resources (Pearcy, 1992; Magnusson and Hilborn, 2003). High rates of natural mortality have been attributed to the ocean entry transition (Parker, 1971; Bax, 1983), yet we still have a poor understanding of the processes governing this mortality. Several mechanisms have been hypothesized—disruption of freshwater hydrological conditions, degradation of estuarine nursery conditions, and interannual variability of predator abundance and prey resources in the marine environment (Levings and van Densen, 1990; Willette, 2001; Logerwell et al., 2003).

Comprehensive management of salmon fisheries, including their conservation and recovery, requires detailed understanding of juvenile salmon ecology during this critical transition. Increased understanding of feeding relationships and potential density-dependent effects, such as diet overlap among co-occurring species and resource limitation could allow for a more ecologically based approach for rebuilding threatened salmon stocks. Specifically, species interactions and their response to variability in prey resources could be important factors for predicting marine survival and the forecasting of adult returns (Logerwell et al., 2003).

Juvenile salmon have been documented feeding in a variety of habitats, including freshwater (Keeley and Grant, 2001; Hampton et al., 2006), estuaries (Healey, 1980; Murphy et al., 1988; Reese et al., 2009), and in the coastal ocean (e.g., Brodeur and Pearcy, 1990; Daly et al., 2009). Inland marine waters (e.g., bays, straits, sounds, fjords, etc.) have been characterized less frequently (Sturdevant et al., 2004; Romanuk and Levings, 2005; Saito et al., 2009). Like estuaries, these inland marine salmon habitats are more geographically and ecologically diverse than offshore habitats, and thus it may be more difficult to generalize about juvenile salmon feeding ecology in these areas.

Dabob Bay, a temperate marine fjord in Puget Sound, northwestern Washington, has been the site of numerous studies of plankton dynamics

(e.g., Frost, 1988; Bollens et al., 1992a, 1992b; Frost, 2005 and references therein). Although these studies have provided extensive insight into zooplankton population dynamics and predator-prey interactions, none has specifically reported on the seasonality of zooplankton community composition from this area. Four juvenile salmon species reside in Dabob Bay temporarily during outmigration to the Pacific Ocean (Bollens and Frost, 1989): *Oncorhynchus keta* (chum), *O. tshawytscha* (Chinook), *O. gorbuscha* (pink), and *O. kisutch* (coho). Diets of these four species in the fjord have not been described. Feeding habits of juvenile chum salmon in neritic waters have been described for a nearby location in Hood Canal (Simenstad and Salo, 1980) and feeding habits of juvenile salmon in other nursery areas of Puget Sound have also been described (Simenstad et al., 1982; Duffy et al., 2005).

Much of our understanding of juvenile salmon feeding ecology in northeast Pacific marine waters has been based on detailed analyses of stomach contents, but has been limited by a lack of corresponding analyses of prey fields. Some recent studies have identified the importance of prey selectivity as a factor in assessing the trophic ecology of salmon during early marine residence (Landingham et al., 1998; Schabetsberger et al., 2003). Furthermore, the highly variable diets demonstrated within and between studies indicate that temporal (seasonal, interannual, and interdecadal) and spatial scales of variability are important, and therefore pose a significant challenge for the design of field studies. The result has been an incomplete understanding of juvenile salmon response to dynamic zooplankton prey fields, particularly during one of the most critical life-history stages, i.e., the early ocean transition phase (Beamish and Mahnken, 2001).

Our objectives were 1) to investigate the diet composition of four salmon species (*Oncorhynchus* spp.) collected from two stations (nearshore-shallow and central-basin–deep) in Dabob Bay over three years and several seasons; 2) to determine salmon feeding selectivity (i.e., their diet in relation to prey availability); and 3) to explore potential resource competition among these species during their early marine residence.

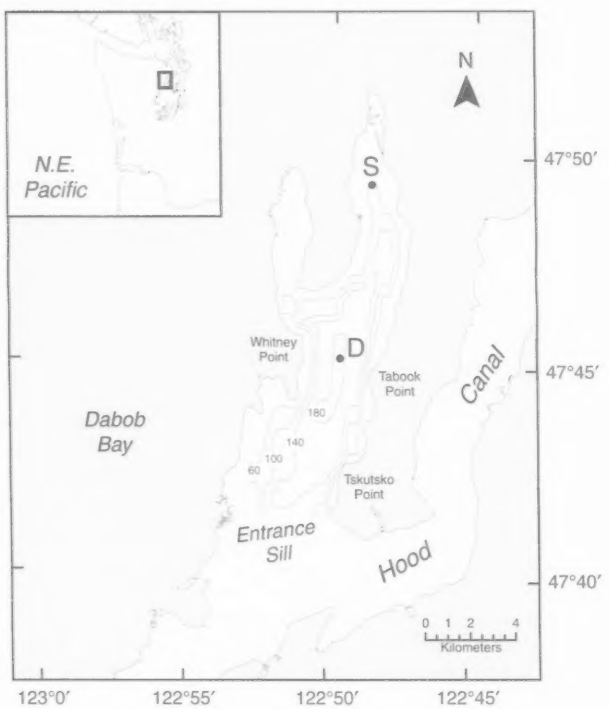

Figure 1

Map of Dabob Bay, Washington. Four species of juvenile Pacific salmon—chum (*Oncorhynchus keta*), Chinook (*O. tshawytscha*), coho (*O. kisutch*), and pink (*O. gorbuscha*)—and zooplankton were sampled at two stations between April 1985 and October 1987 to examine salmon diet, zooplankton availability, feeding selectivity, and potential competition for prey. D=location of the deep (190-m) central bay tstation, and S=the location of the shallow (60-m) nearshore station.

Materials and methods

Fish collection and processing

Between May 1985 and October 1987 we sampled two stations in Dabob Bay, WA (47°45′–50′N lat., 122°50′W long.): a deep (190 m), central station, and a shallow (60 m), nearshore station 9 km apart (Fig. 1). Fish were sampled at night (just after dusk, i.e., when there was no apparent daylight) with two gear types: a midwater trawl with a mouth area of 81.0 m^2 (9.0×9.0 m), and a surface tow net with a mouth area of 18.3 m^2 (3.0×6.1 m) (see Bollens and Frost, 1989 for details). The midwater trawl was towed obliquely from a 50-m depth to the surface at a mean speed of 150 cm/s. Because of concerns about possible avoidance of this net by fish in the upper few meters of the water column (e.g., due to ship wake and propeller wash), we also deployed the surface tow net in the upper three meters of the water column, towed at a mean speed of 80 cm/s behind (50 m) and between (at a midpoint of 50 m) two different vessels (one vessel 5 m and one 15 m in length). Fish were collected at each station during each of four seasons (spring: April–May; early summer: June–July; late summer: August; and autumn: October) in each of three years (1985–87), except for spring of 1985, when no fish were collected (Table 1).

Fish collected with the midwater or surface trawls were sorted and counted, and the catch was weighed by species, lengths were measured, and then individuals of five predetermined size (fork length [FL]) classes (≤49 mm, 50–74 mm,

Table 1

Number of juvenile Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), and pink (*O. gorbuscha*) salmon stomach samples and zooplankton samples collected during 12 visits to each of two stations in Dabob Bay, Washington, 1985–87. Sampling dates are grouped by year within season, number of samples for the deep (D, 190 m) station are indicated on the left and those for the shallow (S, 60 m) station indicated on the right. Diet samples were pooled from midwater trawl and surface trawl collections at each station for each date or dates; duplicate zooplankton samples were collected at each station on each date by vertical hauls of plankton nets. Fish samples were not collected in spring of 1985.

	Number of juvenile salmon stomachs								Number of zooplankton samples	
	Chinook		Chum		Coho		Pink			
Season and sampling dates	D	S	D	S	D	S	D	S	D	S
Spring										
1985									2	2
30 Apr and 29 May 1986	0	0	16	15	0	0	3	7	2	2
6–7 May 1987	0	0	6	10	0	0	0	0	2	2
Subtotal	0	0	22	25	0	0	3	7	6	6
Early summer										
19–20 Jun 1985, 24–25 Jun 1985, 26 Jul 1985	5	10	14	9	0	0	0	0	2	2
4–5 Jun 1986	4	3	10	4	5	1	0	0	2	2
17–18 Jun 1987, 13 Jul 1987	3	5	0	14	1	2	0	0	2	2
Subtotal	12	18	24	27	6	3	0	0	6	6
Late summer										
19–20 Aug 1985, 26–27 Aug 1985	4	5	10	12	0	0	0	0	2	2
12 Aug 1986, 14 Aug 1986	5	7	7	3	0	0	0	0	2	2
19–20 Aug 1987	11	6	7	0	1	0	0	0	2	2
Subtotal	20	18	24	15	1	0	0	0	6	6
Autumn										
7–9 Oct 1985	0	6	5	0	0	0	0	0	2	2
22 Oct 1986	6	10	7	0	0	0	0	0	2	2
14–15 Oct 1987	29	3	3	0	0	0	0	0	2	2
Subtotal	35	19	15	0	0	0	0	0	6	6
Total	67	55	85	67	7	3	3	7	24	24

75–99 mm, 100–149 mm, ≥150 mm) were removed and 0.5–3.0 cc of undiluted formaldehyde were injected into their gut cavity to halt digestion. Each fish was then stored in dilute (5%) formalin-seawater solution. Fish from both trawl types were combined to yield a representative sample of fish residing in the upper 50 m of the water column at night. Subsequently, each fish was weighed (g, wet weight) and measured in the laboratory, and its stomach excised. Stomach contents were weighed (wet weight), digestion stage was recorded, and then prey were identified to the lowest possible taxon (often to species), and enumerated and weighed (wet weight) by category. Diet composition was summarized as the normalized average percent prey biomass ([biomass of taxonomic group]/[total weight of stomach – the weight of the unidentified portion of the stomach contents]). A total of 294 salmon stomachs were examined; six were empty and were not considered further.

For ease of comparison, we pooled the original 122 prey taxa observed into 13 categories that made up at least 10% of any one fish's total normalized prey biomass. Data were stratified by salmon species and size class, season, and station across the three years pooled. In most cases the pooled data were a good representation of the three individual years of data, but in some cases there were interesting interannual differences, as discussed below.

Collection and processing of zooplankton

Zooplankton collections were made at the two stations within 1–2 hours of the fish trawls by using a 1-m^2 mouth opening and 333-μm mesh multiple net sampler (Frost, 1988) in 1985 and 1986 and a 1-m diameter mouth opening and 216 μm mesh Puget Sound net (Research Nets Inc., Seattle) (Miller et al., 1977) in 1987. Duplicate zooplankton samples were collected at each station and on each date (Table 1). A subsample (collected with a Stempel pipette) of 1–2% of the animals was taken and the species were enumerated and

identified for all dates and stations at which fish were collected. Identification of gelatinous animals was generally poor because of their damage during collection. Abundances (densities) were calculated from the subsample counts and volumes (m^3) of water filtered (as measured by a flow meter). Data from different depth strata were weighted by the size (height, m) of the depth strata and then averages for the upper 50 m were computed. Zooplankton community composition was described by station by using the data from duplicate zooplankton tows to compute average abundances for each taxonomic group for each of four seasons (spring, early summer, late summer, and autumn) over the three years studied (1985–87). Dry weights (g/m^2) for zooplankton ≥216 μm were measured as described in Bollens et al. (1992b).

For ease and clarity of presentation of the zooplankton compositional data, the category "other Copepoda" that is used in presenting juvenile salmon gut contents was partitioned into several subcategories, i.e., the genera *Oithona*, *Metridia*, and *Pseudocalanus*. In addition, several taxonomic groups that were common in salmon gut contents were rarely or never observed in the zooplankton samples (e.g., Insecta and Araneae, Cephalopoda, Teleostei, and Ctenophora) and were therefore placed into the "other" category for characterizing zooplankton community composition.

Data analysis

We estimated interspecific diet overlap between co-occurring juvenile salmon species on the basis of biomass of prey in common, using Schoener's (1970) percent similarity index (PSI):

$$PSI_{x,y} = 100\left(1 - 0.5\left(\sum \left|P_{x,i} - P_{y,i}\right|\right)\right), \quad (1)$$

where $P_{x,i}$ = percent biomass of food category (i) in the stomach of species x; and
$P_{y,i}$ = percent biomass of food category (i) in the stomach of species y.

We first pooled the prey biomass data by size class for each salmon species. PSI calculations were made for the subset of samples with a minimum of three stomachs per species. We examined intraspecific spatial variation in diet by calculating the PSI of juvenile salmon between the two stations. PSI values ≥60% were considered significant (Brodeur and Pearcy, 1992; Landingham et al., 1998).

Prey selectivity by juvenile salmon species was examined by using Ivlev's (1961) electivity index (E_i):

$$E_i = (r_i - p_i) / (r_i + p_i), \quad (2)$$

where E_i = the electivity index;
r_i = the numerical proportion of the i^{th} taxon in the stomachs; and
p_i = the proportion of the same taxon in the environment.

The electivity values provide a species-specific measure of prey selection by allowing a comparison of salmon gut contents to available prey. Values for E_i range from –1 to 1, where 1 indicates the highest selectivity (i.e., present in the diet, but never in the zooplankton samples), and –1 indicates lowest selectivity (i.e., never in the diet, but present in the zooplankton samples). We summarized these observations as average species-specific electivity scores for all size classes, seasons, and years combined to compare selection across salmon species.

We compared juvenile salmon gut fullness (% body weight) and zooplankton abundance (dry weight) at each station, as well as each salmon species' gut fullness between the two stations, using Spearman's rank correlations (Zar, 1999). The difference in mean zooplankton abundance (dry weight) between the two stations was tested by using a Mann-Whitney U test (Zar, 1999).

Results

Juvenile salmon diet

Juvenile salmon in Dabob Bay showed species-specific patterns of occurrence throughout the April–October time period across years. In general, more and smaller juvenile salmon were caught at the nearshore shallow station during spring and early summer, and more and larger juvenile salmon were caught at the central-bay deep station during late summer and autumn. Chum salmon were most prominent during the spring and early summer, whereas Chinook salmon were caught more frequently later in the year, particularly at the deep station (190 m). All four salmon species were predominantly planktivorous, although there were some exceptions as described below. Because of the greater occurrence of chum and Chinook salmon diet samples, our analyses were focused on these two species.

Juvenile chum salmon

Chum salmon exhibited striking ontogenetic and spatial variation in diets, including a tendency for fish <100 mm FL to consume more insects and larvaceans and those >100 mm to consume more amphipods and decapod larvae. At the deep station in late spring, euphausiids were the dominant prey type by weight (Fig. 2). Small (≤49 mm) fish also consumed insects, arachnids, and copepods other than *Calanus pacificus*, whereas larger fish (75–99 mm) consumed high percentages of teleosts (primarily unidentified species), hyperiid amphipods, and decapod larvae. The single fish of the 50–74 mm size range captured during early summer at the deep station consumed mostly insects and arachnids, whereas fish between 75 and 150 mm consumed predominantly larvaceans and hyperiids. The single large fish (≥150 mm) contained exclusively euphausiids. In late summer at the deep station, fish 100–149 mm consumed mostly hyperiid amphipods, whereas fish ≥150 mm consumed

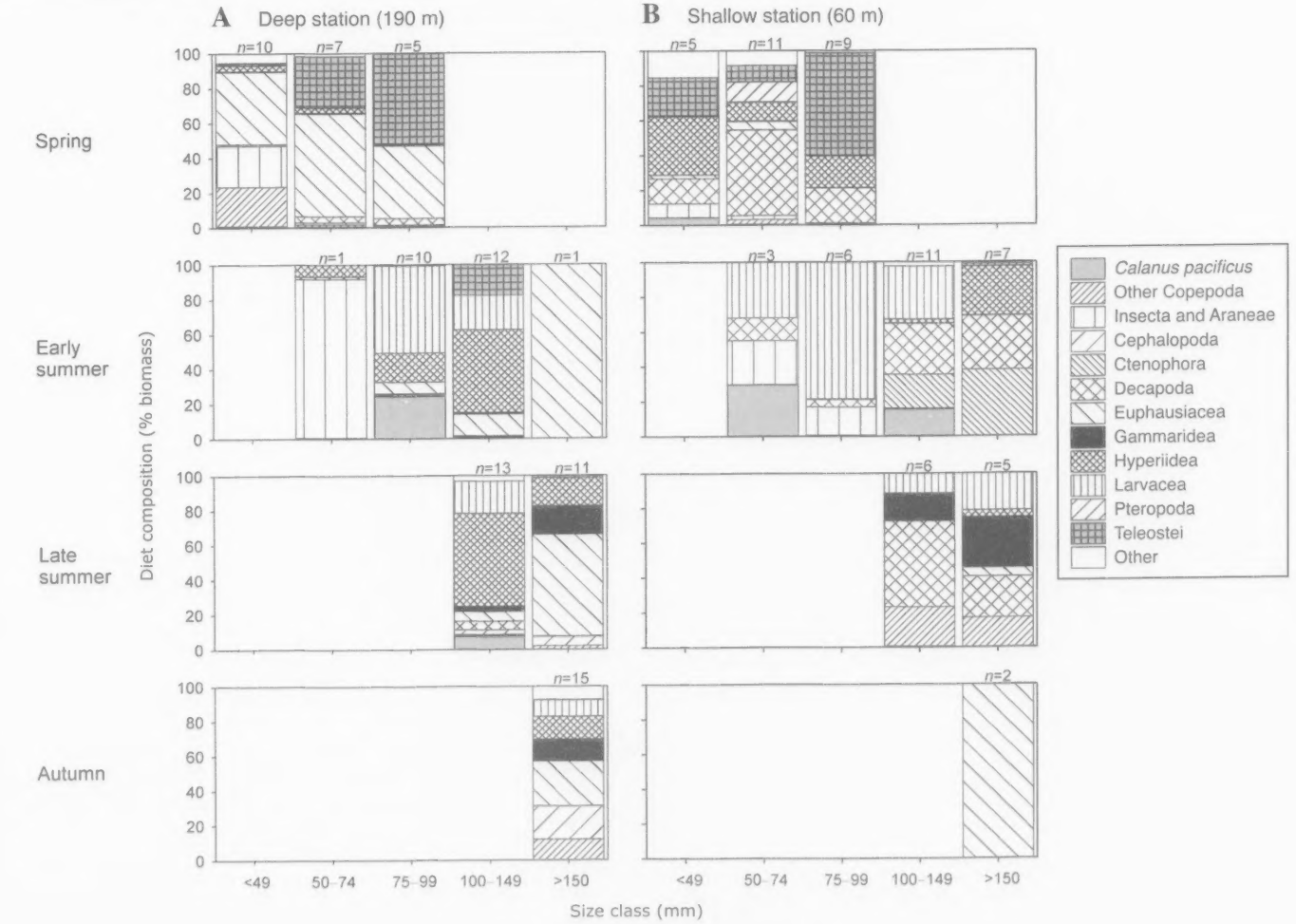

Figure 2

Stomach contents of juvenile chum salmon (*Oncorhynchus keta*) caught at the deep station (**A**) and shallow station (**B**) of Dabob Bay, Washington, during different seasons. Collections were made with a midwater trawl and a surface tow net at each station on each date. Data were pooled over three years (1985–87) for each season and calculated as the normalized biomass of each taxonomic group.

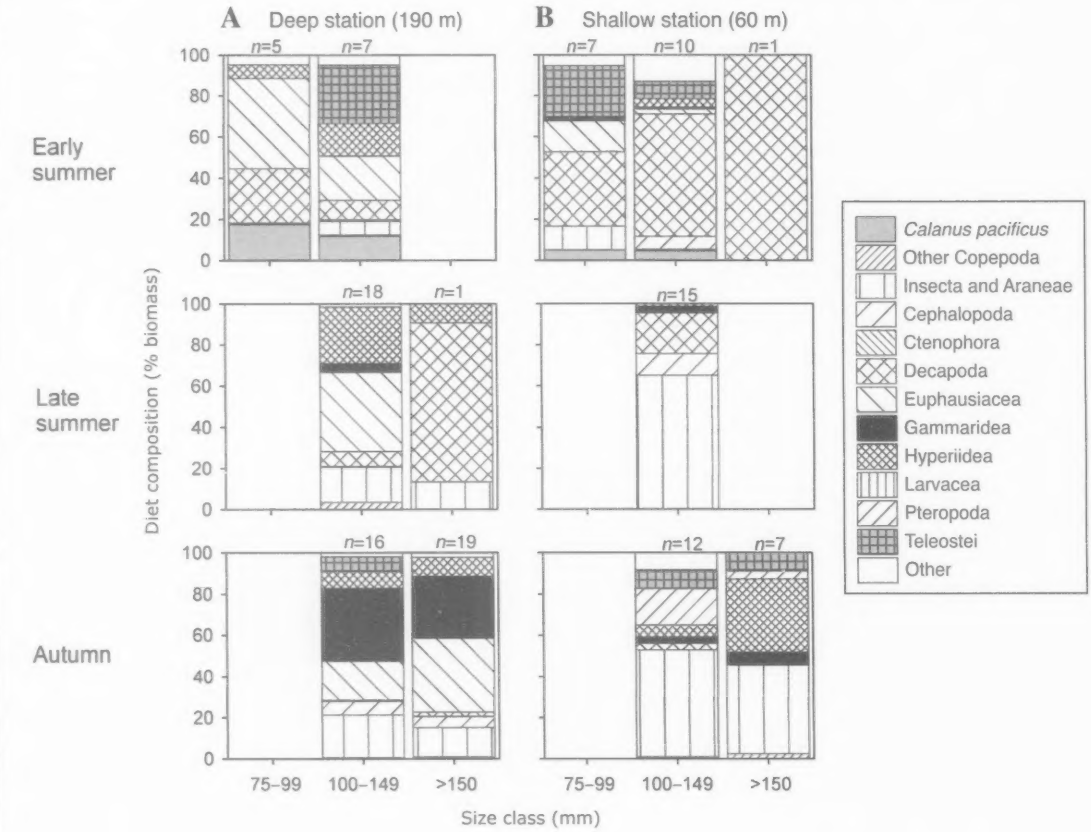

Figure 3

Stomach contents of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) caught at the deep station (**A**) and shallow station (**B**) of Dabob Bay, Washington, during different seasons. Collections were made with a midwater trawl and a surface tow net at each station on each date. Data were pooled over three years (1985–87) for each season and calculated as the normalized biomass of each taxonomic group.

mostly euphausiids, and the remainder consumed mainly gammarid and hyperiid amphipods. In autumn, the diet of fish ≥150 mm from the deep station was composed more evenly of several prey categories, including euphausiids, copepods other than *C. pacificus*, gammarid and hyperiid amphipods, larvaceans, and cephalopods.

In contrast, prey of chum salmon <150 mm at the shallow station were more varied, and few euphausiids were present (Fig. 2B). Teleosts and larvaceans, however, were represented in similar proportions to those at the deep station. Larger chum salmon (>100 mm) sampled in early summer were the only group that consumed relatively large amounts of ctenophores; the remainder of their prey consisted mainly of decapod larvae and hyperiids. During late summer at the shallow station, chum salmon consumed decapod larvae, gammarid amphipods, copepods other than *C. pacificus*, and larvaceans. Large fish (≥150 mm) collected in autumn fed almost entirely on euphausiids.

Juvenile Chinook salmon

There was substantial variation in Chinook salmon diets across size classes, seasons, and stations. At the deep station during early summer, euphausiids constituted a large proportion of the diet of Chinook salmon between 75 and 99 mm (Fig 3A). Fish 100–149 mm consumed a more evenly distributed mix of prey, dominated by teleosts and euphausiids. In late summer, fish 100–149 mm at the deep station consumed mostly hyperiid amphipods and euphausiids. In autumn, fish >100 mm at the deep station consumed mostly gammarids, euphausiids, insects, arachnids, cephalopods, and hyperiids.

At the shallow station in early summer, decapod larvae dominated the diet of Chinook salmon ≥75 mm (Fig. 3B). During both late summer and autumn, insects and arachnids dominated the diets of all three size classes of Chinook salmon, but in autumn, those Chinook salmon >150 mm also consumed hyperiid amphipods.

Diet of other salmon species

Fewer diet samples were available for juvenile pink and coho salmon than for juvenile chum and Chinook salmon. Diet samples of pink salmon were available only for small fish (<49 mm) in spring. At the deep station these fish contained about 50% euphausiids, and gammarids, copepods other than *C. pacificus*, insects, and arachnids made up the other 50%. At the shallow station, their diet included a variety of prey consisting mainly of teleosts, pteropods, copepods other than *C. pacificus*, and fewer insects, decapod larvae, gammarids, and "others." The "others" in this case were mostly bivalves, whereas the "others" for the co-occurring juvenile chum salmon were mostly chaetognaths.

A few juvenile coho salmon were also caught at the two sample stations. At the deep station, diet of coho salmon 100–149 mm consisted primarily of decapod larvae and euphausiids, and a single larger (>150 mm) coho salmon consumed mostly decapod larvae in early summer and another large coho, only gammarid amphipods in late summer. At the shallow station, three coho salmon were caught in June: one (75–99 mm) consumed about 75% "other" taxa (mostly the ostracod *Euphilomedes)*, and the two other fish consumed almost exclusively decapod larvae (like the five co-occurring Chinook salmon).

Juvenile salmon gut fullness in relation to zooplankton abundance

Juvenile salmon gut fullness (% body weight) was not related to zooplankton abundance (dry weight) (Fig. 4; Spearman's rank correlation, $P>0.05$). For all four species of salmon, gut fullness was generally greater in spring and early summer and declined somewhat during late summer and autumn (chum salmon at the deep station in 1985 was an exception to this). In contrast, zooplankton dry weight at the deep station peaked in the fall, and minima occurred in the spring. At the shallow station, peaks in zooplankton dry weight tended to occur in the summer, and less pronounced minima occurred in spring and autumn. Zooplankton dry weight was substantially greater at the deep station than at the shallow station ($P<0.001$, Mann-Whitney U test; Zar, 1999), generally by one order of magnitude. Some of this difference may have been due to the three-fold greater water column depth at the deep station, whereas a generally larger part of this difference was due to greater abundances of large-body zooplankton in the deep station samples. In addition, no significant correlation was found for individual salmon species' gut fullness at the two different stations (Spearman's rank correlation, $P>0.05$; Zar, 1999).

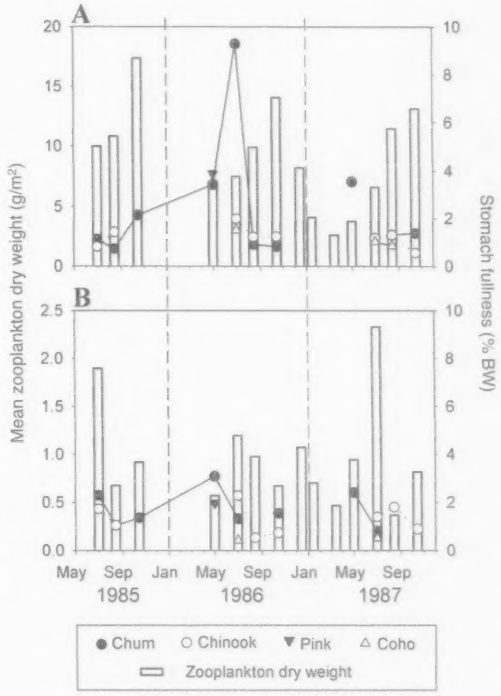

Figure 4

Zooplankton (≥216 µm) dry weights (g/m²) and fish stomach fullness (mean % body weight) for four species of Pacific salmon—chum (*Oncorhynchus keta*), Chinook (*O. tshawytscha*), pink (*O. gorbuscha*), and coho (*O. kisutch*)—sampled between April 1985 and October 1987 at a deep station (**A**) and a shallow station (**B**) in Dabob Bay, Washington. Fish collections were made with a midwater trawl and a surface tow net, and zooplankton collections were made with vertical hauls of a plankton net at each station on each date. Dashed vertical lines separate years. Note the different scales for zooplankton dry weights on the two y axes.

Community composition of zooplankton

Zooplankton communities (upper 50 m at night) were numerically dominated by copepods at both stations (Fig. 5). The most striking contrast between our zooplankton composition and our juvenile salmonid diet composition was the far greater abundance of copepods in the zooplankton. Substantially different seasonal patterns in zooplankton community composition were observed between stations during 1985 and 1986, but not in 1987. At the deep station, the greatest species richness was typically observed during early spring, whereas two species—*Metridia lucens* and *Calanus pacficus*—dominated

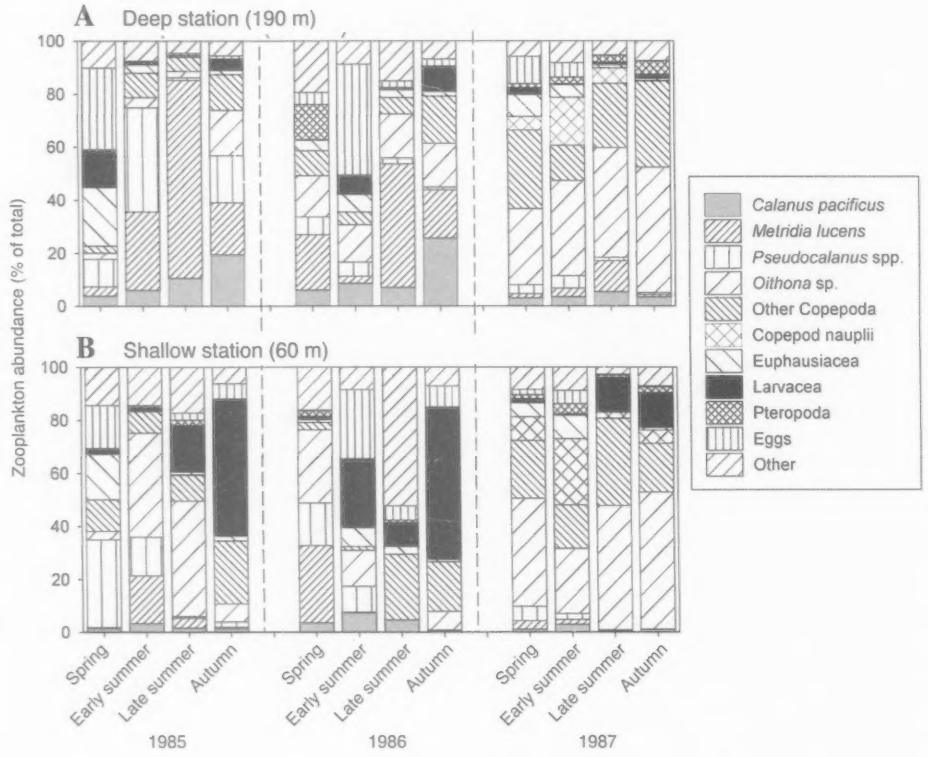

Figure 5

Composition of zooplankton in the upper 50 meters at night at a deep station (**A**) and a shallow station (**B**) in Dabob Bay, Washington. Zooplankton collections were made with duplicate vertical hauls of a plankton net at each station during each of the four seasons during 1985, 1986 and 1987. Dashed vertical lines separate years.

in summer and autumn. In contrast, *Oithona* sp. and larvaceans dominated the shallow station in summer and autumn. In 1987, however, zooplankton community composition between the two sites was remarkably similar (Fig. 5) and was dominated by *Oithona* sp. and "other Copepoda" (predominantly unidentified stages 1 and 2 calanoid copepodites) throughout the entire sampling period.

Electivity indices for juvenile salmon

All salmon species consistently and strongly selected for insect, arachnid, and cephalopod prey (E_i>0.75) and routinely selected against *Calanus pacificus*, copepods other than *C. pacificus*, ctenophores, larvaceans and pteropods (E_i<–0.25). All salmon species except pink salmon typically selected for decapod prey (0.25< E_i<0.75; both caridean shrimp and brachyuran crab larvae were present in the spring, but brachyurans dominated the decapod prey in summer). Hyperiid amphipods and teleosts were generally selected for by chum and Chinook salmon (0.25<E_i<0.75) but were consumed in proportion to their relative abundance or were selected against by coho and pink salmon (–0.75<E_i<0.25). Euphausiids were generally neutrally selected (–0.25<E_i<0.25). However, electivity scores varied substantially within a given salmon species. For example, in 26 Chinook salmon diet samples, electivity indices for euphausiid prey ranged from –1.0 to 0.99 (data not shown), but were not consistently related to predator size, season, or prey abundance.

Important ontogenetic changes in prey-selection behavior were revealed by size-specific electivity values (Fig. 6). For instance, smaller size chum salmon strongly avoided larvacean prey, whereas larger chum (>75 mm) showed roughly neutral or positive selectivity. Similarly, small (75–99 mm) Chinook salmon tended to avoid gammarid amphipods, whereas larger individuals (>100 mm) tended to select gammarids. Also, smaller Chinook salmon individuals tended to consume *Calanus pacificus* at rates proportional to their abundance in the environment, but the larger Chinook salmon strongly avoided these prey. In general, it seemed that larger fish

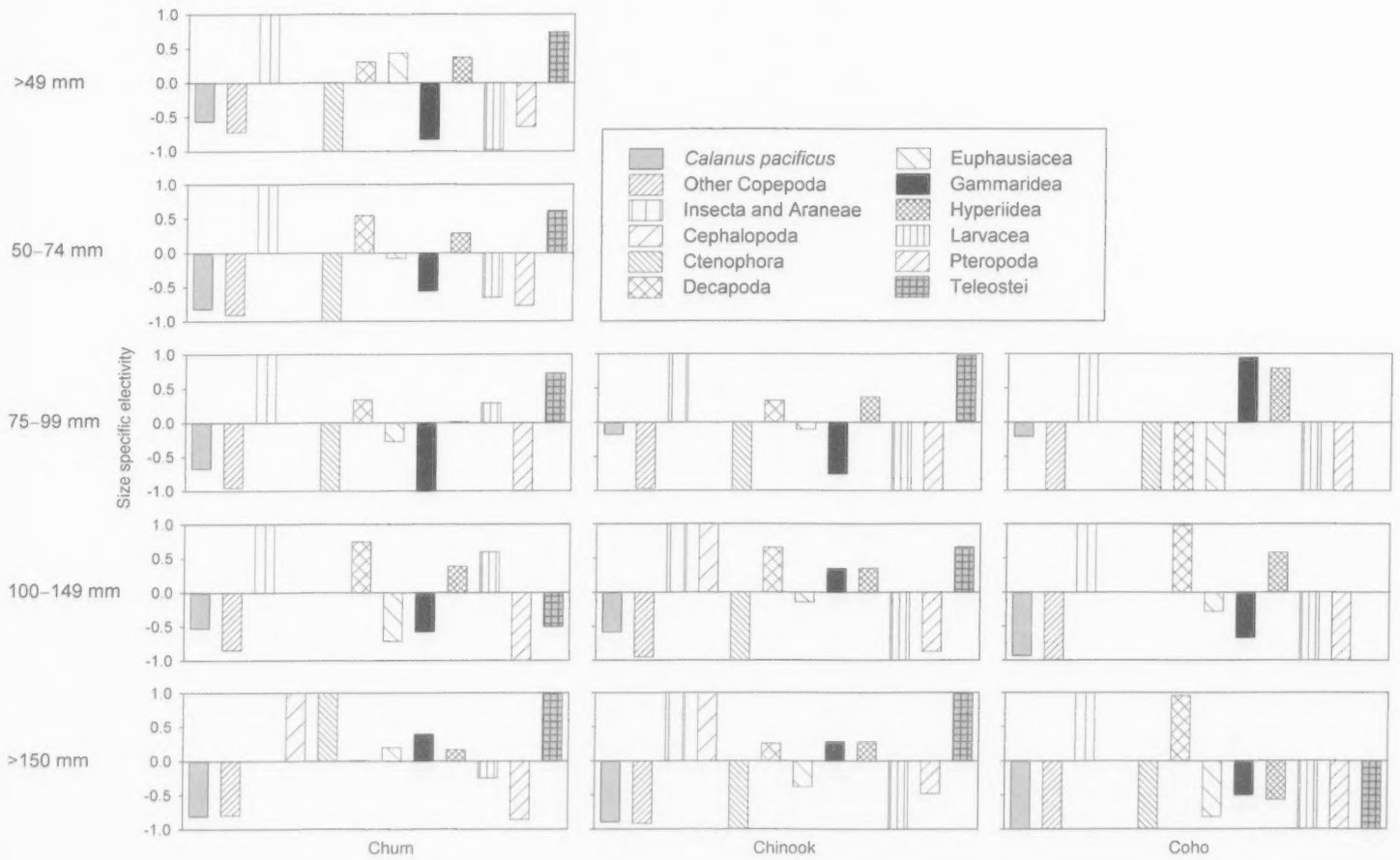

Figure 6

Size-specific (mm fork length) electivity indices (E_i) for chum (*Oncorhynchus keta*), Chinook (*O. tshawytscha*), and coho (*O. kisutch*) salmon at Dabob Bay, Washington. Fish collections were made with a midwater trawl and a surface tow net, and zooplankton collections were made with vertical hauls of a plankton net at each station on each date. Electivity indices were pooled over all seasons (early spring to autumn), both stations (190-m and 60-m deep), and years (1985–87).

selected for larger prey. However, prey selection by coho and pink salmon showed little ontogenetic variation, although we had far fewer data for these taxa to make a definitive statement. Patterns of prey selectivity were fairly similar between stations for each juvenile salmon species, although there were occasionally some differences, e.g., for 100–149 mm Chinook salmon, which selected euphausiids at the deep station but avoided them at the shallow station.

Juvenile salmon diet overlap

Juvenile salmon diets rarely overlapped significantly. Diet overlap for the most frequently co-occurring (n=11 hauls) species, chum and Chinook salmon, ranged from 10.5% to 66.8%, and averaged 38.3%. PSI was significant only on June 1985 and August 1987, when both species consumed euphausiids, hyperiid amphipods, and *C. pacificus*. We observed the greatest diet overlap between coho and Chinook salmon, which both ate decapod prey in June 1986 and 1987, for an average PSI of 77.9%. Diet similarities varied for the other juvenile salmon species and were based on only one or two co-occurrences. For juvenile chum and coho salmon, the PSI was only 10.8%; for juvenile pink and chum salmon, the PSI was 58.9% in April 1986.

Salmon diets also varied spatially; however, the PSI was not significant for any of the 13 intraspecific comparisons between stations, and averaged only 26.5%. Chinook salmon PSI was approximately 30% (n=7), and that of chum (n=5) and pink (n=1) salmon was <20%.

Discussion

Juvenile salmon diets, zooplankton abundance and composition, and salmon feeding selectivity in Dabob Bay exhibited considerable spatial, seasonal, and interannual variability. Some notable patterns and trends were nevertheless evident, and provide important implications for our understanding of feeding ecology and potential resource competition among juvenile salmon as they migrate from nearshore environments to more open waters.

Food resources and salmon gut fullness

Dramatic differences in the zooplankton communities between the deep water and nearshore stations occurred in two of three years. The most striking difference was the greater biomass of zooplankton, often an order of magnitude higher, at the deep station compared to the shallow station (Fig. 4; Bollens et al., 1992b), primarily because of the greater abundance of large, vertically migrating zooplankton at the deeper station (e.g., euphausiids and large calanoid copepods). Because zooplankton biomass represents a measure of overall food abundance (although see below for an alternative interpretation), we expected to see differences in gut fullness between the two stations if juvenile salmon were food limited and did not often migrate between the sites (a distance of 9 km). However, despite this large difference in prey resources between sites, we found no evidence for fuller salmon guts at the deep station. In addition, different zooplankton communities were consistently observed between stations (Fig. 5), which could explain the low diet overlap of each salmon species between stations (mean PSI=27%).

Gut fullness can be a useful indicator of feeding success. However, gut fullness does not account for potential differences in prey nutritional quality (Brodeur, 1992; Armstrong et al., 2008). Given equal gut fullness, feeding success may be greater for fish that consumed a larger proportion of high quality prey than were eaten by congener species. We observed very high gut fullness (9% of body weight) in juvenile chum salmon during early summer 1986, but much of the diet was composed of low-quality food items such as larvaceans. Data on prey quality would enhance future comparisons of juvenile salmon diets and gut fullness.

Electivity patterns and ontogeny

The nearshore feeding ecology of the earliest marine stages of juvenile salmon <100 mm has been studied well in the past (e.g., Kaczynski et al., 1973; Sturdevant et al., 1996), and juvenile salmon feeding ecology, species-specific feeding preferences, and prey selection for fish >100 mm in length captured in highly variable nearshore coastal environments have been examined in more recent studies (Moulton, 1997; Landingham et al., 1998; De Robertis et al., 2005, Armstrong et al., 2008). Ours is one of few studies where larger juvenile fish from transitional inland marine habitats have been examined (Willette, 2001; Sturdevant et al., 2004; Armstrong et al., 2008).

A variety of zooplanktivorous fish select prey disproportionate to their abundance in the environment (e.g., Lazzaro, 1987; Gerking, 1994). For salmon and other fishes, these patterns have been attributed to multiple factors, including: prey size (Brodeur, 1991); prey pigmentation or other visual indicators (Peterson et al., 1982; Schabetsberger et al., 2003); and vertical migration behavior of predator and prey (Bollens and Frost, 1989; Viitasalo et al., 2001). Our three-year study of juvenile salmon feeding in Dabob Bay provides additional evidence that juvenile chum, Chinook, coho, and pink salmon exhibit ontogenetic shifts in prey size selection and that they select for larger and more visually conspicuous prey. Previous studies showed that diel vertical migration is an important mediator of planktivore trophic interactions in Dabob Bay (e.g., Bollens and Frost, 1989; Frost and Bollens, 1992; Bollens et al., 1993).

Juvenile salmon in Dabob Bay used a diverse prey field and demonstrated species-specific prey preferences. Chum and Chinook salmon both highly preferred insects, cephalopods, decapod larvae, hyperiid amhipods,

and teleost prey. Coho and pink salmon both strongly selected for insects, whereas decapod larvae were important to the former and gammarid amphipods to the latter. Our study supports the importance of insect prey to young juvenile salmon in transitional environments (Moulton, 1997; Romanuk and Levings, 2005; Weitkamp and Sturdevant, 2008).

The diet of juvenile chum salmon further differed from the other salmon species by the abundance of larvaceans (primarily *Oikopleura* sp.) in their gut contents, and their consumption of ctenophores. These observations are consistent with other reports (Simenstad and Salo, 1980; Black and Low, 1983; Landingham et al., 1998) and may be related to anatomical gut specialization, which enables chum salmon to assimilate prey items that other salmon cannot digest (Welch, 1997; Arai et al., 2003).

Calanoid copepods have been described as a major diet item for juvenile salmon generally (Pearcy, 1992), and for chum and pink salmon specifically (Godin, 1981; Sturdevant et al., 2004). However, despite a diverse and abundant assemblage of copepod species in Dabob Bay, copepods only represented a modest component of our salmon diets and were particularly limited to smaller predators. Instead, juvenile salmon in Dabob Bay were found more often feeding on numerically less abundant macrozooplankton such as euphausiids, hyperiid amphipods, and decapod larvae. Similarly, Peterson et al. (1982) showed that juvenile coho and Chinook salmon off Oregon fed more on hyperiid amphipods than on the numerically dominant copepods. These results support the results from other studies that indicate that salmon are more likely to feed on larger, more visible prey items (Healey, 1980; Schabetsberger et al., 2003), in which case abiotic factors (e.g., light intensity and turbidity) and biotic processes (e.g., vertical migration and predator evasion behavior) will be important variables that will help determine stomach fullness and feeding success.

Ontogenetic diet thresholds for juvenile salmon at approximately 80 mm, before which teleost prey are less important, have been indicated by other studies (Brodeur, 1991; Keeley and Grant, 2001). In contrast, our electivity results provide evidence that teleost prey were strongly selected for by small (<75 mm) chum and pink salmon during spring, when fish larvae may have been particularly small (Bollens et al., 1992a; Fulmer and Bollens 2005). Simenstad and Salo (1980) found that juvenile chum salmon transitioned from nearshore habitats with epibenthic food sources to neritic habitats with pelagic and nektonic food sources when they reached approximately 45–55 mm FL. In other studies, seasonal variability in salmon gut contents has been attributed to ontogenetic shifts in feeding preferences or feeding behavior (Beacham, 1986; Brodeur, 1991; Daly et al., 2009). Similarly, our results indicate that small chum, Chinook, and coho salmon select small prey, then larger prey as the fish develop. Small Chinook and coho salmon selected *Calanus pacificus* roughly in proportion to its abundance, but other copepods were avoided. Similarly, only small coho salmon selected gammarid and hyperiid amphipods. In contrast, only large Chinook salmon selected for gammarids. Thus, both species-specific and ontogenetic shifts in prey preference were observed.

Our diet and electivity results should be interpreted cautiously because our samples were pooled across broad size, temporal, and spatial scales, and because of limitations associated with sample sizes, net sampling biases, and pooling of prey species and life history stages. For example, the range of euphausiid electivity values observed may be due to the pooling of euphausiid species and life-history stages, potentially obscuring euphausiid prey selection patterns observed in other studies (Schabetsberger et al., 2003).

Another major caution concerns our ability to determine "available prey" with plankton nets. More mobile and larger nektonic prey, such as cephalopods and young fish, are able to avoid conventional plankton nets, with the consequence that electivity indices for these prey types would be biased upward. Conversely, small prey types that are unable to avoid the plankton net (e.g., small copepods) would be proportionately overrepresented in the net samples, with the consequence that electivity indices for these forms would be biased downward. We recommend that further research be undertaken into adequately sampling macrozooplankton and micronekton (e.g., Gewant and Bollens, 2005), such that a broader and potentially more appropriate range of potential prey for fishes can be quantitatively sampled.

Several additional complicating factors should be considered when interpreting electivity indices. First, strongly positive electivity (e.g., E_i=1.00) often results from a rare presence of a species in the gut contents and a corresponding absence of that same species in the plankton. In some cases zero abundance in the plankton may be due to low-volume plankton hauls which under-sample the available prey field. Conversely, an E_i of –1.00 could result from a rare (but nonzero) occurrence of a species in the environment, combined with its absence from the gut contents, perhaps simply because of a low probability of encounter between predator and prey.

A final caution concerns the vertical resolution of sampling. Landingham et al. (1998) used both neuston and oblique plankton tows and showed that salmon diet most closely resembled that of the neuston assemblage. The upper 50 m were sampled with our sampling methods and therefore electivity values may have been biased. For example, if juvenile salmon are primarily feeding near the surface, abundant zooplankton (i.e., copepods) that are more deeply distributed may not fully be part of the "available" prey community. We recommend finer-scale, vertically resolved sampling of juvenile salmon and their potential prey in future studies.

Dabob Bay has been the site of numerous studies for which the interactions between planktivorous fishes and

the behaviors exhibited by their potential prey have been explored (Ohman, 1986; Frost, 1988; Bollens and Frost, 1989; Bollens et al., 1992a; Bollens et al., 1993). Field studies by Bollens and Frost (1989) indicated that abundances of actively feeding planktivorous fish (including *Oncorhynchus* spp.) are directly linked with the strength and timing of vertical migration exhibited by the copepod *Calanus pacificus*. Our results indicate that the adaptive response exhibited by species such as *Calanus pacificus* seems to be an effective mechanism for avoiding predation by species such as juvenile salmon. Thus, "available" prey items are not only those that are abundant or of the desired size, but those that are also available for visual detection. Availability may be affected by the prey's presence or absence from the photic zone, or by the presence of pigmentation that makes the prey more detectable visually. Most of the prey items that were consistently consumed by salmon in this study (e.g., euphausiids, hyperiid and gammarid amphipods, and decapod larvae) possess characteristically dark or large eyes. The ability of salmon to detect these potential prey items may be increased by heavy pigmentation, large body size, and their frequently noted association with the near surface layer (Lough, 1976; Peterson et al., 1982) where salmon typically feed.

Diet overlap and potential interspecific competition among salmon species

A variety of studies have relied on diet overlap as a primary indicator of potential resource competition between co-occurring species. Although there is little consensus among studies of salmon, diet overlap has been most frequently observed between Chinook and coho salmon in Oregon and Washington (Peterson et al., 1982; Emmett et al., 1986; Brodeur and Pearcy, 1990; Brodeur, 1991), and to a lesser extent between chum, pink, and sockeye salmon (*Oncorhynchus nerka*) in British Columbia and Southeast Alaska (Healey, 1980; Beacham, 1993; Landingham et al., 1998). Our results from Dabob Bay show the greatest spatial and temporal overlap between chum and Chinook salmon but also provide evidence only for resource partitioning (low diet overlap) between these two species, not necessarily competition (which would require resource limitation).

In contrast, our data show significant diet overlap between Chinook and coho salmon (average PSI=77.9%), supporting earlier reports of potential resource competition between these two species. Although Brodeur and Pearcy (1990) did not see evidence for significant overlap between four salmon species when all observations were combined, they observed significant overlap between Chinook and coho salmon during May and June, as well as during the 1983 El Niño. Likewise we found that significant overlap between Chinook and coho salmon occurred during June (of 1986 and 1987), largely because of the shared consumption of decapod larvae, which are visually conspicuous and seasonally abundant at this time of year. However, the co-occurrence of juvenile Chinook and coho in Dabob Bay was less prominent than in coastal Oregon (Peterson et al., 1982; Brodeur and Pearcy, 1990; Brodeur and Pearey, 1992); however, our results are based on far fewer data.

Despite the co-occurrence of different juvenile salmon species in Dabob Bay, and the occasional occurrence of significant diet overlap between these species, we did not see any indication of food limitation. That is, there was never a significant relationship between stomach fullness and zooplankton biomass, as might be expected if food was limited. However, just as with the electivity indices discussed above, we caution that our vertical plankton net hauls may not adequately sample the potential prey of juvenile salmon. Testing for food limitation by correlating salmon stomach fullness and the abundance of potentially more appropriate prey (e.g., macrozooplanktonic, micronektonic, and neustonic prey) would prove interesting, but was not possible given our sampling method. Similarly, our comparison of zooplankton dry weights with salmon stomach wet weights complicates the interpretation of food limitation and potential competition because conversions from wet-weight to dry-weight would be expected to vary between prey taxa (e.g., between gelatinous and crustacean prey).

Resource limitation by juvenile salmon during their early marine transition may be influenced by several other factors not addressed in our study, including direct and indirect effects of hatchery production in the region (Quinn et al., 2005) and potential diet overlap with other zooplanktivores (Purcell and Sturdevant, 2001). Furthermore, zooplankton dynamics in temperate marine waters are clearly influenced by interannual (El Niño cycles) and interdecadal (Pacific Decadal Oscillation) scales of climate variability (Mackas et al., 2001; Hooff and Peterson, 2006) and there are important linkages to salmon survival during multiple life-history stages (Beamish and Bouillon, 1993; Logerwell et al., 2003). Although diet data from our three-year study could be averaged across years (as opposed to size classes, etc.), interannual climate factors cannot be overlooked. Indeed, based on a multivariate El Niño–Southern Oscillation index (MEI), 1987 ranks as a moderate to strong El Niño year (April–October MEI average=1.91), and likewise represents the most anomalous year of our study for seasonal plankton composition in Dabob Bay. This was particularly apparent at the deeper station, where the abundance of *Oithona* sp. and larvaceans seemed to be more characteristic of the shallow, nearshore station in 1985 and 1986. Mechanisms underlying the interannual variability of zooplankton composition in Dabob Bay warrant further exploration.

Our combination of detailed analyses of prey fields and fish diets is clearly only one approach to understanding juvenile salmon feeding ecology. Biochemical methods of studying energetics and feeding relationships (e.g., Johnson and Schindler, 2009) provide additional insight into juvenile salmon trophic dynamics. Studies across the variety of habitats encountered by salmon during their outmigration and early residence in marine environments will be necessary to fully un-

derstand species-specific responses to resource and environmental variability. Our results from Dabob Bay indicate that periodic high diet overlap between salmon species may occur. However, evidence of resource partitioning, especially between frequently co-occurring species (e.g., chum and Chinook salmon), combined with a lack of evidence for food limitation (although this should be more explicitly tested in the future), indicates that competition between juvenile salmon is unlikely to occur in this marine fjord.

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Movement patterns of winter flounder (*Pseudopleuronectes americanus*) in the southern Gulf of Maine: observations with the use of passive acoustic telemetry

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Abstract—Despite its recreational and commercial importance, the movement patterns and spawning habitats of winter flounder (*Pseudopleuronectes americanus*) in the Gulf of Maine are poorly understood. To address these uncertainties, 72 adult winter flounder (27–48 cm) were fitted with acoustic transmitters and tracked by passive telemetry in the southern Gulf of Maine between 2007 and 2009. Two sympatric contingents of adult winter flounder were observed, which exhibited divergent spawning migrations. One contingent remained in coastal waters during the spawning season, while a smaller contingent of winter flounder was observed migrating to estuarine habitats. Estuarine residence times were highly variable, and ranged from 2 to 91 days (mean=28 days). Flounder were nearly absent from the estuary during the fall and winter months and were most abundant in the estuary from late spring to early summer. The observed seasonal movements appeared to be strongly related to water temperature. This is the first study to investigate the seasonal distribution, migration, and spawning behavior of adult winter flounder in the Gulf of Maine by using passive acoustic telemetry. This approach offered valuable insight into the life history of this species in nearshore and estuarine habitats and improved the information available for the conservation and management of this species.

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Winter flounder (*Pseudopleuronectes americanus*) is a commercially and recreationally important flatfish species that is distributed along the east coast of North America from North Carolina northward to Newfoundland (Bigelow and Schroeder, 1953). Within U.S. waters, this species is managed as three stock units: the southern New England and Mid-Atlantic (SNE–MA); Gulf of Maine; and Georges Bank. To date, there has been less research on the Gulf of Maine stock than on the SNE–MA stock. Seasonal distribution patterns of winter flounder in the Gulf of Maine have emerged from fisheries catch data (McCracken, 1963), mark recapture experiments (Perlmutter, 1947; Howe and Coates, 1975) and annual trawl surveys. However, these sources of data offer limited insight into patterns of estuarine residence and nearshore habitat use for winter flounder because trawl fisheries and research surveys in the Gulf of Maine are typically limited to coastal and offshore waters. In addition, these traditional sampling sources for obtaining distribution data cannot identify individual variability in movement or spawning behavior. In the present study, we sought to investigate spawning patterns and seasonal distribution of winter flounder in nearshore and estuarine waters in the southern Gulf of Maine using passive acoustic telemetry.

The magnitude of variability in individual migration patterns remains poorly understood for even the most economically valuable fish species (Able and Grothues, 2007), in part because we have yet to recognize the importance of contingent behavior. Contingents are cohesive groups of fish within a population that exhibit a common migration pattern (Cadrin and Secor, 2009). Acoustic telemetry offers new opportunities to investigate the fine-scale movements and behavior of individual fish. This technology allows for the recognition of contingent groups within populations (Secor, 1999) and offers insight into the amount of connectivity between estuarine and coastal populations (Able, 2005). Acoustic telemetry has been used to gather high resolution data on the behavior of juvenile winter flounder in the Gulf of Maine (Fairchild et al., 2009). However, before the present study, this technology had not been used to study adult winter flounder in the Gulf of Maine.

Traditionally, winter flounder spawning in the Gulf of Maine was thought to be restricted to estuarine habitats (Bigelow and Schroeder, 1953). This assumption was subsequently reflected in designations of Essential Fish Habitat (EFH) for this species (NMFS, 1999). However, other observations indicate that winter flounder in the Gulf of Maine also use coastal waters as spawning grounds (i.e., Howe and Coates, 1975). If a proportion of in-

dividuals spawn in coastal, rather than estuarine habitats, these fish would represent contingents within the larger population. Contingents may provide populations with enhanced stability and resilience because of the variable survival rates of early life history stages in different habitats (Secor, 2007; Kerr et al., 2010). Divergent spawning migrations increase the distribution of eggs and larvae, which may reduce the probability of a failed recruitment event (Lambert, 1990). For winter flounder that spawn demersal eggs, the conditions encountered by the early life history stages are largely determined by the locations where the adults spawn. Therefore, divergent spawning migrations may have a large effect on the recruitment success of local populations.

We chose to monitor adult winter flounder in Plymouth Bay and the adjacent Plymouth Harbor, Kingston Bay, and Duxbury Bay estuary. Plymouth Harbor, Kingston Bay, and Duxbury Bay estuary are commonly referred to as the Plymouth Estuary, and that name will be used throughout this article. Winter flounder is a dominant member of the groundfish community in the Plymouth Estuary, and the estuary serves as an important nursery area for this species (Lawton et al., 1984). Winter flounder are known to spawn in the Plymouth Estuary, where peak spawning occurs in March and April (Entergy[1]). In addition, Plymouth Bay has been identified as an area where coastal spawning likely occurs (NMFS, 1999).

The goal of this study was to obtain high-resolution data on the seasonal distribution, migrations, and spawning behavior of winter flounder in the southern Gulf of Maine. In particular, three primary objectives were addressed during this study: 1) to determine if adults in this region exhibit divergent spawning migrations; 2) to investigate the seasonal distribution of winter flounder in the region, in association with water temperature; and 3) to compare the seasonal distribution observed in this study to that observed in past research in the Gulf of Maine where static sampling methods were used.

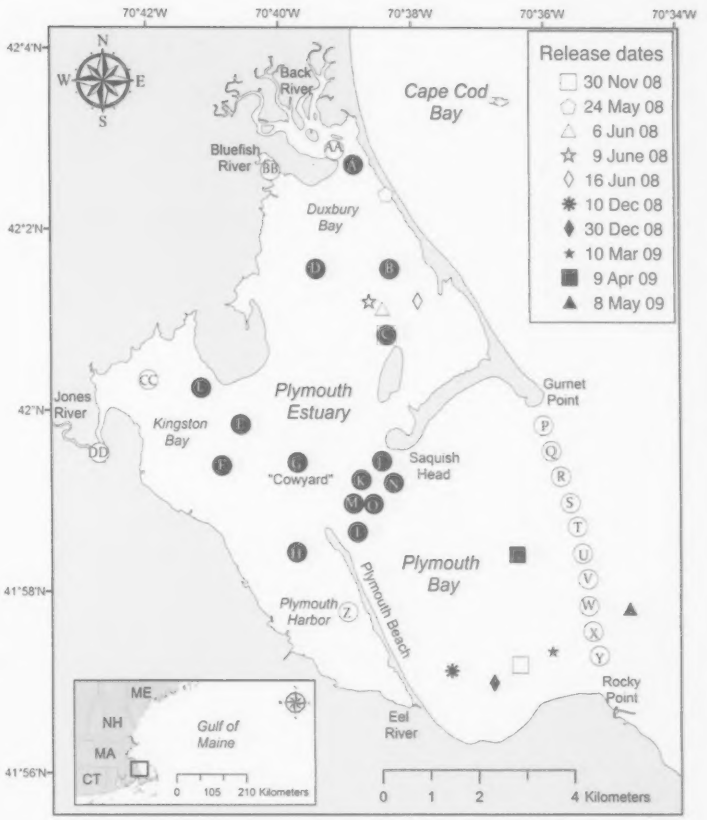

Figure 1

Map of the study site showing the locations of Plymouth Bay and Plymouth Estuary in the Gulf of Maine where the movements of winter flounder (*Pseudopleuronectes americanus*) were tracked with passive acoustic telemetry. Locations of tag releases and acoustic receivers are shown. Receivers used to track winter flounder movements from November 2007 to November 2008 are shown as solid black circles and receivers added to the array in December 2008 are shown as open circles. Circles are not drawn to scale and do not represent the detection radii of acoustic receivers.

Materials and methods

Study site

The Plymouth Estuary and Plymouth Bay are located in the southern portion of the Gulf of Maine (Fig. 1). The Plymouth Estuary is bordered on its seaward side by two barrier beaches. Tidal exchange between the Plymouth Estuary and Plymouth Bay occurs through a 2020-m opening between Saquish Head and the northern extremity of Plymouth Beach. The estuary is well mixed and approximately 66% of the water is replaced during each tidal cycle, creating strong tidal currents (Davis, 1984). Plymouth Bay is bordered by Cape Cod Bay to the east.

The average depth within Plymouth Estuary is 3.3 m at mean high water and 2.1 m at mean low water, and

[1] Entergy. 2001. Ichthyoplankton entrainment monitoring at Pilgrim Nuclear Station, January–December, 2000. *In* Marine ecology studies related to operation of Pilgrim Station. Report no. 57, 65 p. Entergy Nuclear Generation Company. Plymouth, MA.

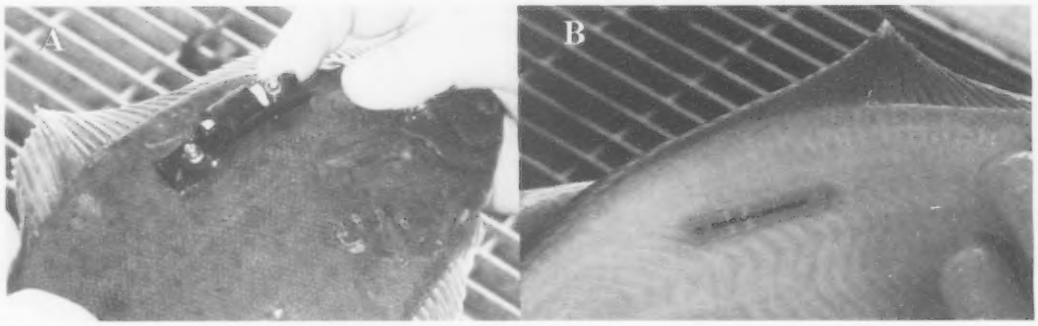

Figure 2

An example of the external attachment method that was used to secure the acoustic transmitters to winter flounder (*Pseudopleuronectes americanus*) to monitor their movements in the southern Gulf of Maine. The Vemco V92L transmitters were fitted into a harness of 9/16" soft latex tubing and secured in the harness with two-part epoxy (**A**). Two nickel tagging pins were passed upwards through the blind side of the fish, through the dorsal musculature (**B**).

salinity in the estuary ranges from 0.0 to 33.0 (Iwanowicz et al.[2]). The bathymetry of the estuary is complex, and extensive sand and mud flats are exposed at low tide when the surface area of the estuary is reduced from 10,057 acres to 5465 acres (Iwanowicz et al.[2]). A deeper channel is present between Saquish Head and Plymouth Beach, where depths reach nearly 26 m. There are four main sources of freshwater input to the Plymouth Estuary: the Back River, Bluefish River, Jones River, and Eel River.

Acoustic telemetry

Adult flounder were captured by using either a small otter trawl, a commercial trawl vessel, or by hook and line. Sampling was nonrandom, and sampling locations were chosen from areas where adult winter flounder have historically been abundant. Tow times with the small otter trawl varied from 10 to 30 minutes, and tows with the commercial vessel were 30 minutes in duration. The total length of each fish was measured to the nearest centimeter, and only adult fish ($\geq$27 cm) in good or excellent condition were fitted with acoustic tags. After tagging, fish were held onboard for observation until they were deemed healthy enough for release. All fish were released in close proximity to the capture site in order to minimize tagging-induced stress.

In total, 72 adult winter flounder (27–48 cm) were fitted externally with acoustic transmitters (model V92L, 69 kHz, 9 mm×21 mm, Vemco Ltd., Halifax, NS, Canada) between November 2007 and May 2009. Each transmitter had an average pulse rate of 80 seconds (range=40–120 seconds) and an expected battery life of 384 days. A novel external attachment method was developed for this study. Acoustic transmitters were secured into a harness of 9/16 inch (14.3 mm) soft latex tubing by using two-part epoxy (Fig. 2). Two nickel tagging pins were passed upwards from the blind side of the flounder through the dorsal musculature. The harness was then secured to the nickel pins on the eyed-side of the fish with plastic earring backings. The tagging procedure took an average of two to three minutes per fish. A laboratory holding study indicated 100% transmitter retention and 100% survival over a seven-month period. A separate holding study conducted at the University of New Hampshire in 2009 indicated that the tag attachment method did not interfere with the swimming or spawning behavior of tagged fish (E. Fairchild, personal commun.[3]).

In November 2007, 24 prespawning winter flounder were tagged in Plymouth Bay, approximately 5 km from the mouth of the Plymouth Estuary (Fig. 1). Three of these winter flounder were observed to be gravid females at the time of release. Repeated efforts were made to capture spawning flounder within the estuary during March, April, and early May of 2008, but we were not able to capture adult fish until late May 2008. Twenty three adult winter flounder were tagged within the Plymouth Estuary between 24 May and 16 June 2008 (Fig. 1). In the second year of the study, an additional 25 winter flounder were tagged in Plymouth Bay between December 2008 and May 2009 (Fig. 1). Eight winter flounder tagged on 8 May 2009 were observed to be gravid females that were in spawning condition.

[2] Iwanowicz, H. R., R. D. Anderson, and B. A. Ketschke. 1974. A study of the marine resources of Plymouth, Kingston and Duxbury Bay. Monograph Series Number 17, 37 p. Division of Marine Fisheries, Boston, MA.

[3] Fairchild, Elizabeth. 2009. Department of Biological Sciences, Univ. New Hampshire, Durham, NH 03824.

Winter flounder tagged between November 2007 and June 2008 (n=47) were tracked within the Plymouth estuary by using a moored array of 15 wireless receivers (model VR2 and VR2W, Vemco Ltd.; Fig. 1). Six of these receivers (I, J, K, M, N, and O; referred to as the "inner gate") were configured as a parallel curtain that spanned the mouth of the Plymouth estuary, allowing the movements of fish traveling between Plymouth Bay and Plymouth estuary to be recorded precisely. Parallel curtain arrays are advantageous because they allow the direction of movement for each fish to be obtained (Heupel et al., 2006). Range testing was performed at the mouth of the estuary by placing transmitters on the bottom in different locations for ten-minute intervals. After range testing, receivers within the parallel curtain were positioned to ensure that overlap existed between the detection radii of adjacent receivers. Tagged winter flounder were monitored within the upper reaches of the Plymouth estuary by using nine receivers positioned in a nonoverlapping grid array. These receivers were placed within the deeper channels of the Plymouth estuary to maximize their detection radii.

During the second year of the study, the receiver array was expanded from 15 to 30 wireless receivers (Fig. 1). Ten receivers (P–Y; referred to as the "outer gate") were deployed across the mouth of Plymouth Bay, from Gurnet Point in Duxbury southward to Rocky Point in Plymouth. This arrangement allowed us to track the movement of tagged winter flounder between Cape Cod Bay and Plymouth Bay. An additional five receivers (Z–DD) were placed within the upper reaches of the Plymouth estuary. Expanding the receiver array allowed us to test more directly our hypotheses about the spawning behavior of the 25 winter flounder that were tagged between 10 December 2008 and 8 May 2009.

Before their retrieval in 2009, six of the 30 acoustic receivers were lost, likely because of boat traffic, interactions with commercial fishing gear, or because of winter storms. Receivers P and Y were lost from the outer gate between Cape Cod Bay and Plymouth Bay. Receivers I, M, and O were lost from the parallel curtain between Plymouth Bay and the Plymouth estuary. Subsequently, receiver G was moved from the "Cowyard" and placed adjacent to the position of receiver M to improve the coverage in this area. Receiver H in Plymouth Harbor was also lost, likely because a high volume of boat traffic in the area.

Data analysis

The movement track of each tagged fish was visualized by using GIS software (ArcMap vers. 9.3, ESRI, Redlands, CA). Estuarine residence time was calculated as the time elapsed between the first and last detection for each individual within the Plymouth estuary. If a tagged winter flounder was recorded within the estuary on more than one occasion, the total days spent within the estuary during each visit were combined to calculate residence time for that individual.

Winter flounder were classified as either estuarine or coastal spawners on the basis of their observed locations during the peak spawning months of March through May. Fish that were detected within the Plymouth estuary at any time over this three month span were classified as estuarine spawners, whereas winter flounder that remained in coastal waters were classified as coastal spawners. A G-test for independence (Sokal and Rohlf, 2001) was performed to examine whether significant interannual variability was present in the proportion of tagged winter flounder that were classified as estuarine spawners in 2008 and 2009. The ratio (with 95% confidence intervals) of estuarine to coastal spawners observed over the two-year period was calculated (Sokal and Rohlf, 2001).

Abiotic monitoring

During the study, bottom water temperature was monitored at four locations within the study site. Three temperature loggers (Vemco Ltd.; 8-bit minilog TR) were attached to the moorings of receivers A, E, and K within the Plymouth Estuary. These temperature loggers were placed 0.5 meters above the bottom and were programmed to record bottom water temperature every 30 minutes. A temperature logger placed in the southeastern portion of Plymouth Bay recorded bottom water temperature once every two hours in 2007 and 2008. In September 2008, another temperature logger was placed on the mooring of receiver T to record bottom temperature in Plymouth Bay. In 2009 some of the temperature loggers failed. When available, bottom water temperature data were averaged weekly at each site.

Results

With passive acoustic telemetry, we successfully gathered high-resolution data on the migration, spawning behavior, and seasonal distribution of adult winter flounder in the southern Gulf of Maine. Twenty eight of the 47 winter flounder tagged during the first year of the study were later detected within the Plymouth estuary, yielding a total of 16,956 detections in our array of acoustic receivers. Twenty two of the 25 fish tagged during the second year of the study were later detected in the receiver array, resulting in 97,394 unique detections. A summary of data for each tagged winter flounder that was later detected is given in Table 1.

Spawning behavior

Based on the observed movements of tagged winter flounder during the spawning season, the presence of two contingent spawning groups of flounder was evident in the region: coastal spawners and estuarine spawners. In both years of the study, the majority of tagged winter flounder exhibited coastal spawning behavior. Only five of the 24 winter flounder (21%) tagged in Plymouth Bay in 2007 were classified as estuarine spawners. Seven of

Table 1

Summary of information for tagged winter flounder (*Pseudopleuronectes americanus*) that was detected during the study. For each tagged winter flounder, the date of release and date of last location are given. The total number of detections, and receivers at which that winter flounder was detected, is provided. For the release locations, PB=Plymouth Bay and PE=Plymouth Estuary.

Tag ID	Length (cm)	Release date	Release location	Last detection	No. of detections	Receiver stations
5837	34	11/30/2007	PB	8/26/2008	27	Outer Cape
5839	28	11/30/2007	PB	10/30/2008	63	C,F,G,N
5850	30	11/30/2007	PB	11/19/2008	2030	C,J,K,M,N,O
5852	32	11/30/2007	PB	6/1/2008	735	J,K,N,O
5862	29	11/30/2007	PB	6/12/2008	100	C,D,K,M,O
5867	36	11/30/2007	PB	5/28/2008	1	K
5868	34	11/30/2007	PB	8/25/2008	1458	J,K,M,N,O
5877	32	11/30/2007	PB	6/22/2008	799	E,F,G,I,M,O
5832	29	5/24/2008	PE	6/17/2008	44	B,C,J
5833	27	5/24/2008	PE	9/30/2008	3227	B,C,J,K,N
5840	33	5/24/2008	PE	6/10/2008	1681	C,J
5844	27	5/24/2008	PE	6/12/2008	957	C,J,K,M,O
5845	35	5/24/2008	PE	6/13/2008	338	C,J,N
5847	42	5/24/2008	PE	7/30/2008	3198	C,J,K,M,N,O
5855	36	5/24/2008	PE	5/26/2008	90	D
5858	29	5/24/2008	PE	6/15/2008	30	K,M
5859	35	5/24/2008	PE	7/7/2008	18	C,J,N
5866	42	5/24/2008	PE	6/15/2008	119	A,C,J
5873	27	5/24/2008	PE	6/13/2008	267	B,K,M
5878	35	5/24/2008	PE	6/13/2008	217	B,C,J
5835	39	6/6/2008	PE	6/10/2008	55	J,K,M,O
5846	30	6/6/2008	PE	6/21/2008	18	C,J
5856	33	6/6/2008	PE	8/18/2008	211	C,J
5864	27	6/6/2008	PE	6/23/2008	27	B,I,M
5874	38	6/6/2008	PE	6/15/2008	636	B,C,J,N
5871	27	6/9/2008	PE	6/14/2008	9	M,O
5876	36	6/9/2008	PE	9/14/2008	546	C,J,K,N,O
5843	28	6/16/2008	PE	10/6/2008	18	C,K
5872	27	6/16/2008	PE	7/24/2008	37	C,N
53876	33	12/10/2008	PB	5/2/2009	10346	G,K,N,X
53877	31	12/10/2008	PB	8/26/2009	6750	G,Q,R,T,U,V,W,X, MA Bay
53879	36	12/10/2008	PB	7/25/2009	19394	V,W,X
53884	36	12/10/2008	PB	5/13/2009	1484	Q,R,S,T,U,V,W,X
53886	31	12/10/2008	PB	7/8/2009	14089	G,K,N,S,T,U
53887	30	12/10/2008	PB	7/20/2009	5061	Q,R,S,T,U,V,W,X
53888	31	12/10/2008	PB	6/14/2009	23842	G,J,K,N,R,S,T,U
53890	29	12/10/2008	PB	6/27/2009	57	X
53891	32	12/10/2008	PB	5/22/2009	443	G,K,N,R,S,T,U.V
53894	41	12/10/2008	PB	7/28/2009	3611	C,E,Q,R,S,T,U,V,W,X
53896	31	12/10/2008	PB	6/26/2009	361	X
53892	37	3/10/2009	PB	6/18/2009	1215	R,U,V,W,X
53893	34	3/10/2009	PB	7/8/2009	288	X
53874	33	4/9/2009	PB	4/11/2009	1061	R,S,T,U
53883	35	4/9/2009	PB	5/4/2009	3018	Q,R,S
53885	31	4/9/2009	PB	7/14/2009	2074	G,K,J,N,Q
53873	39	5/8/2009	PB	5/24/2009	620	Q,U,S,T,U,V,W,X
53875	37	5/8/2009	PB	5/12/2009	177	Q,R,S,T,U,V,W
53878	36	5/8/2009	PB	6/12/2009	2230	G,K,Q,R,S,T,U.X
53881	36	5/8/2009	PB	7/25/2009	479	Q,R,S,T,U,V,W,X
53895	36	5/8/2009	PB	6/25/2009	701	B,C,G,J,N,W,X
53897	48	5/8/2009	PB	5/10/2009	93	V,W,X

the 25 winter flounder (28%) released in Plymouth Bay during 2008 and 2009 were observed to be estuarine spawners. A *G*-test for independence revealed no significant interannual variability (P=0.56) in the ratio of coastal and estuarine spawners between the two years. In total, only 12 of the 49 (25%) tagged winter flounder were noted to be estuarine spawners. The 95% upper confidence limit for this proportion was calculated to be 0.70. If spawning was restricted to estuaries, the proportion of winter flounder classified as estuarine spawners would be one (100%). Therefore, our results demonstrate that in the Plymouth Bay region of the Gulf of Maine, winter flounder spawning is not restricted to estuaries.

Eleven winter flounder were observed to be gravid females at the time of release. Only one of the three gravid females tagged in Plymouth Bay in November 2007 was later detected in the estuary, but not until May of the following year. Eight gravid females were tagged in Plymouth Bay on 8 May 2009. Two of these individuals migrated rapidly to the mouth of the estuary. These females were detected at the mouth of the estuary six and ten days after release, respectively. Whether these individuals spawned in the estuary, or migrated to the estuary after spawning in coastal waters is unknown. It was apparent that the six of eight gravid winter flounder remained in Plymouth Bay after being tagged.

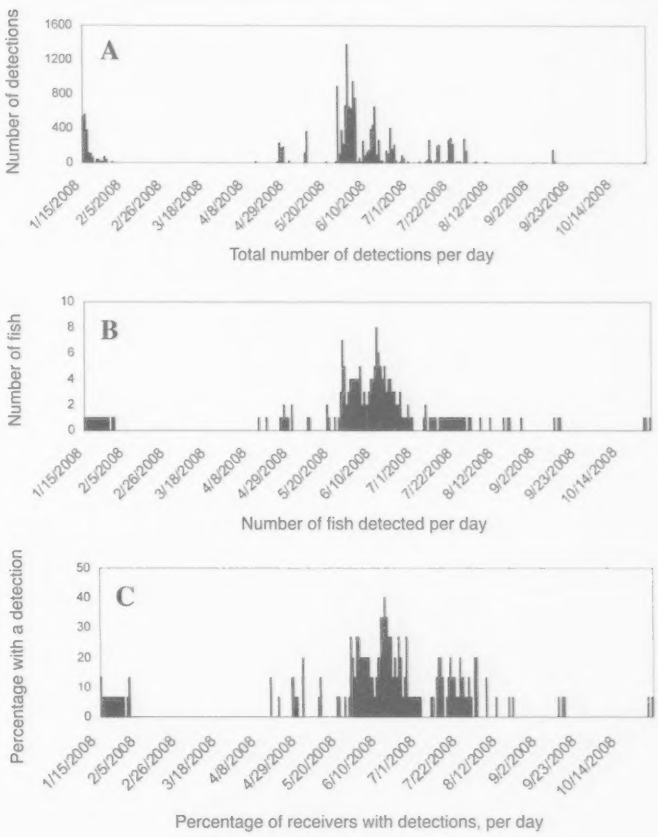

Figure 3

Temporal patterns of winter flounder (*Pseudopleuronectes americanus*) detections obtained by using passive acoustic telemetry in the Plymouth Estuary, MA, between January 2008 and October 2008. (**A**) The total number of detections each day. (**B**) The number of tagged winter flounder that were detected each day. (**C**) The percentage of acoustic receivers that detected a tagged winter flounder during each day of the study.

Seasonal distribution

The seasonal distribution of tagged winter flounder in the Plymouth Bay region became apparent after two years of passive telemetry. Adult winter flounder were largely absent from the Plymouth estuary during the winter months in both years. Only four of the 38 tagged winter flounder at large during the winter of 2008 and 2009 were detected in the Plymouth estuary (Figs. 3 and 4). In the winter of 2008, temperatures were warmer and more stable in Plymouth Bay (range=1.2–5.0°C) than in the Plymouth estuary (range=-1.24–5.2°C) (Fig. 5). In the winter of 2009, the observed temperature ranges were similar in Plymouth Bay (–0.6–5.0°C) and the Plymouth estuary (–0.9–5.9°C).

The movement of winter flounder into the Plymouth estuary began during the spring and was coincident with an increase in water temperature. Some tagged winter flounder began to migrate into the estuary in mid-April, when estuarine temperatures ranged from 9° to 12°C. In 2008, the mean temperature observed when winter flounder migrated from Plymouth Bay in to the Plymouth Estuary was 10.9°C. Tagged flounder were most abundant within the estuary between May and early June (Figs. 3 and 4) when temperatures ranged from 9° to 16°C, and this was also the only period when we were able to capture adult flounder in the estuary. The majority of winter flounder tagged in 2009 remained in the coastal waters of Plymouth Bay in late spring, where water temperatures ranged from 9° to 13°C.

We observed an emigration of tagged winter flounder from the Plymouth estuary during the onset of summer, as water temperatures increased. The mean observed temperature when tagged winter flounder emigrated from the estuary was 13.9°C, and 89% of all recorded

departures from the estuary occurred when bottom temperatures were >12°C. In 2008, 18 of the 23 (78%) winter flounder tagged within the estuary migrated to coastal waters over a three week period from 30 May to 19 June (Fig. 6). This emigration coincided with a sharp increase in water temperature throughout the estuary. As of 19 June 2008, water temperatures exceeded 15°C in all but the deepest portion of the estuary. During July and August of 2008 when temperatures reached their seasonal maxima, no winter flounder were detected in the upper reaches of the estuary, and six winter flounder were detected at the mouth of the estuary, where temperatures were the coolest. In July 2009, only one winter flounder was detected in the estuary, for a period of one day.

Our observations on the autumn distribution of winter flounder in the Plymouth estuary were limited to 2008. Results indicated that five tagged individuals returned to the estuary as water temperatures decreased below their seasonal maxima.

For tagged winter flounder that were detected in the estuary, residence times within the estuary ranged from 2 to 91 days (mean=29 days). The estuarine residence times of fish tagged in Plymouth Bay (mean=40 days) were significantly greater than the residence times for winter flounder tagged in the estuary (mean=22 days) (single-factor ANOVA; P=0.025). No relationship was found between fish size and estuarine residence time (P=0.88). For winter flounder tagged within the Plymouth estuary in 2008, the observed residence time is almost certainly an underestimate because it is unknown how long these fish were present in the estuary before being tagged.

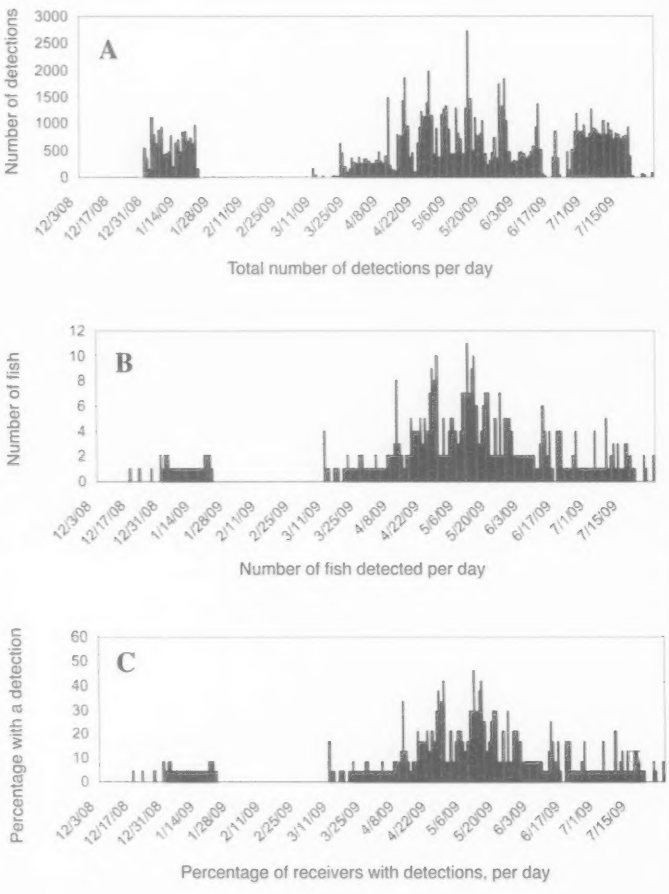

Figure 4

Temporal patterns of winter flounder (*Pseudopleuronectes americanus*) detections obtained by using passive acoustic telemetry in the Plymouth Estuary and Plymouth Bay, MA, between December 2008 and July 2009. (**A**) The total number of detections each day. (**B**) The number of tagged winter flounder that were detected each day. (**C**) The percentage of acoustic receivers that detected a tagged winter flounder during each day of the study.

Detections of tagged winter flounder were not uniformly distributed throughout the study site. In the first year of the study, the inner gate of acoustic receivers typically detected more flounder and had more detections than receivers located within the estuary (Fig. 7, A and B). Tagged winter flounder were detected throughout the estuary, and seven of the nine receivers inside the estuary detected at least one tagged flounder. In the second year of the study, tagged winter flounder were most commonly detected in the coastal waters of Plymouth Bay. The outer gate of receivers in Plymouth Bay typically detected the greatest number of winter flounder and had the largest number of detections (Fig. 7, C and D). Two tagged winter flounder (Tags 53876 and 53886) remained at the inner gate for long periods of time within the detection radii of receivers G and K, which accounted for the large number of detections by these receivers (Fig. 7D). In 2009, tagged winter flounder were detected at only three of the 12 receivers inside the estuary, and the low number of detections (<1000) at these three receivers indicates that residence within the estuary was brief. The bimodal distribution of receiver detections (e.g., Fig. 7C) supports the inference of divergent habitat use, spawning behaviors, and contingent structure.

Two tagged winter flounder were detected at receivers used by other

researchers (W. Hoffman, personal commun.[4]), documenting more substantial movements beyond the study area. One tagged winter flounder (tag 5837) moved from the Gulf of Maine stock area to the SNE–MA stock area and was detected east of Cape Cod on 26 August 2008 (Table 1). This individual was tagged in Plymouth Bay on 30 November 2007 and was never detected in our receiver array. Tag 53877 was detected throughout our array in 2009 and was later detected in Massachusetts Bay on 26 August 2009 (Table 1).

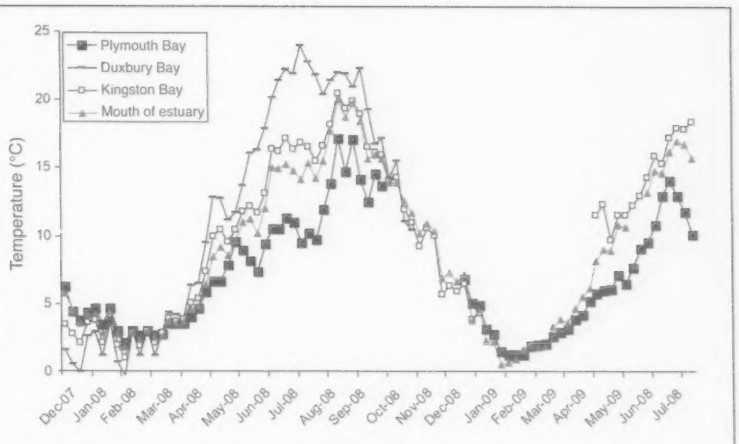

Figure 5

Weekly averaged bottom water temperatures observed between November 2007 and July 2009. Water temperature was recorded every 30 minutes at four locations during the study: Plymouth Bay; the mouth of the Plymouth Estuary; Kingston Bay (western portion of Plymouth Estuary); and Duxbury Bay (northern portion of Plymouth Estuary).

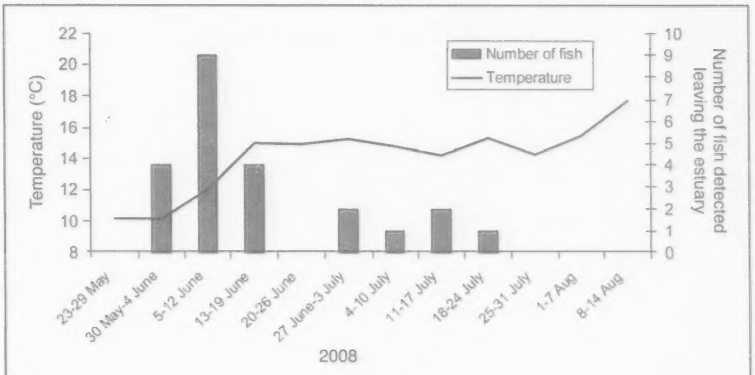

Figure 6

The relationship between water temperature and the emigration of tagged winter flounder (*Pseudopleuronectes americanus*) from the Plymouth Estuary in 2008. Winter flounder emigrated rapidly from the Plymouth Estuary as water temperatures increased from 10° to 15°C at the beginning of the summer.

Receiver efficiency

Despite the loss of some receivers, it appears that the array was efficient for the detection of the migrations of winter flounder. Twenty eight winter flounder released during the first year of the study were later detected in the estuary. Each fish was detected in the estuary an average of 416 times (range=1–3227 detections) at an average rate of 1.9 detections/day at liberty. Seventeen of the 24 winter flounder released in Plymouth Bay were never detected inside the estuary. These 24 winter flounder were released outside the receiver array that was used in the first year (Fig. 1); therefore, if these fish remained in coastal waters they would not have been detected by our array. Twenty two of the 25 winter flounder released in the second year of the study were later detected in our array. On average, each tagged winter flounder was detected 2861 times (range 57–23,842 detections) at an average rate of 14.1 detections/day at liberty. Winter flounder tagged on 8 May 2009, were released slightly eastward of the receiver array (Fig. 1), and this location may explain why two of these tagged fish were never detected again.

In the fall of 2008, receivers I and M were lost from the inner gate of receivers that spanned the mouth of the estuary. After these receivers were lost, two tagged winter flounder (tags 5833 and 5873) were detected inside the estuary at the end of September and October, respectively, without being detected at the inner gate of receivers. One flounder (tag 5855) was released inside the estuary on 24 May 2008, and was detected two days later at receiver D. However, this individual was never detected at another receiver during the study. The fate of this fish is unknown. It may have been captured in the recreational fishery, eaten by another animal, or died after having been tagged. This was the only winter flounder that was released and detected inside the estuary (tag 5855) that was never detected at the inner gate. In the second year of the study, only one tagged winter flounder (tag 53894) that was detected inside

[4] Hoffman, William. 2009. Massachusetts Division of Marine Fisheries, Gloucester, MA 01930.

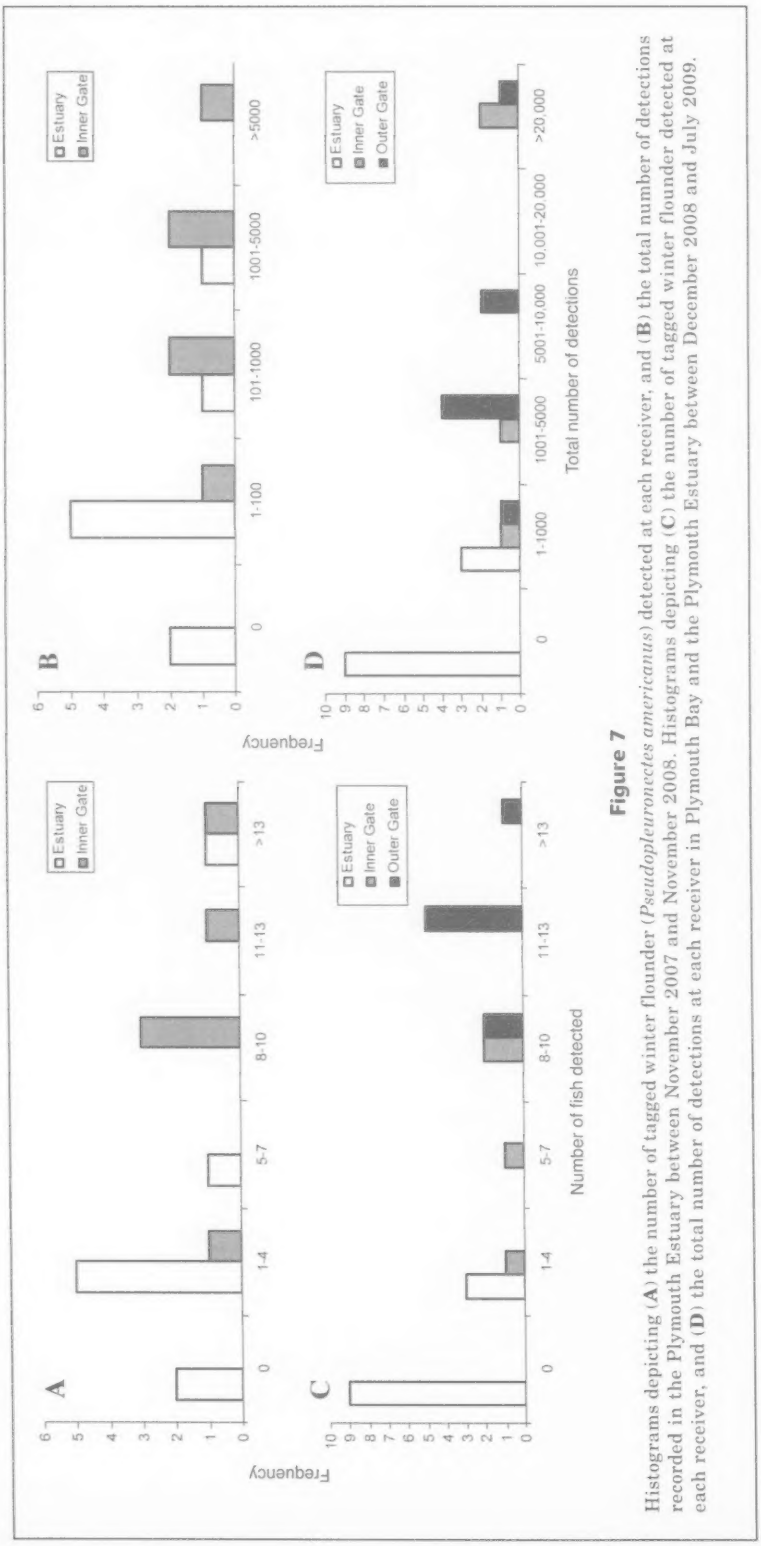

Figure 7

Histograms depicting (**A**) the number of tagged winter flounder (*Pseudopleuronectes americanus*) detected at each receiver, and (**B**) the total number of detections recorded in the Plymouth Estuary between November 2007 and November 2008. Histograms depicting (**C**) the number of tagged winter flounder detected at each receiver, and (**D**) the total number of detections at each receiver in Plymouth Bay and the Plymouth Estuary between December 2008 and July 2009.

of the estuary without first being detected at the inner gate. However, this individual was later detected at the inner gate when it emigrated from the estuary in May.

A quantitative assessment of the efficiency of the outer gate receivers in Plymouth Bay is more difficult. It is unlikely that winter flounder were able to pass between adjacent receivers without being detected, because tagged winter flounder were commonly detected simultaneously at two or three adjacent receivers in Plymouth Bay, indicating that these receivers had overlapping detection radii. Unfortunately, the receivers that were lost (P and Y) were each at the edges of the outer gate. Therefore, it is difficult to assess how many fish may have moved from Plymouth Bay to Cape Cod Bay without being detected.

Discussion

Using acoustic telemetry, we were able observe the movements of adult winter flounder in the southern Gulf of Maine with high spatial and temporal resolution. In particular, we were able to investigate the spawning behavior of tagged winter flounder in the vicinity of Plymouth Bay and assess the seasonal distribution of tagged flounder in the region. This approach yielded valuable insight into the life history of this species.

Spawning behavior of winter flounder

Our observations support the hypothesis that winter flounder spawning in the Gulf of Maine is not restricted to estuaries. Two sympatric contingents of winter flounder were observed, both of which exhibited divergent spawning migrations. The majority of adults tagged in coastal waters (76%) were absent from the estuary during the peak spawning months of March through May. In addition, eight of the eleven tagged winter flounder that were observed to be gravid did not enter the estuary during the spawning period.

Evidence of coastal spawning by winter flounder in Plymouth Bay

was also found in previous studies. Ichthyoplankton sampling has been conducted in this region for decades to assess the impacts of the Pilgrim Nuclear Power Station (PNPS), which is on the southeast shore of Plymouth Bay. Researchers at Marine Research, Inc.[5] used a physical model to estimate the time it would take for eggs spawned in the Plymouth estuary to drift to Plymouth Bay near the power plant. They collected and aged eggs at PNPS and found that a proportion of the eggs had been spawned too recently to have originated from the estuary. They concluded that these eggs had been spawned in Plymouth Bay, rather than the estuary.

Evidence for coastal spawning has also been noted in other regions of the Gulf of Maine. Howe and Coates (1975) suggested that coastal spawning groups may exist on the basis of their observations of tagged flounder captured in coastal and offshore waters during the spawning season. Data collected during the NOAA Northeast Fisheries Science Center annual spring trawl survey have shown that the mean depth occupied by winter flounder in the Gulf of Maine has increased significantly over the last 40 years (Nye et al., 2009). This increase in depth may reflect a broad shift from estuarine to coastal spawning in the Gulf of Maine stock.

Winter flounder do not require estuaries as spawning habitat. This is evidenced by the large, self-sustaining stock of winter flounder that is present on Georges Bank (NMFS, 1999). Rather, estuarine spawning appears to be a strategy to maintain localized population structure. Tagging studies have shown that winter flounder display homing to their spawning grounds (Perlmutter, 1947; Saila, 1961). Dispersal is limited or nonexistent during the egg stage. In addition, larval behavior and estuarine hydrographic features promote the retention of larvae within estuarine spawning areas (Pearcy, 1962; Crawford and Carey, 1985; Chant et al., 2000). These characteristics, which promote local population structure, also make winter flounder vulnerable to human impacts.

Anthropogenic impacts such as dredging, pollution, eutrophication, and elevated temperatures often occur in estuaries (Nelson et al., 1991), and these activities can reduce the survival of winter flounder eggs, larvae, and juveniles. Estuaries are relatively small in size and are more susceptible to changes in water temperature than are coastal waters (Abood and Metzger, 1996). Elevated temperatures have been shown to reduce the survival and fitness of winter flounder eggs (Keller and Klein-MacPhee, 2000) and winter flounder has been identified as a species that is particularly vulnerable to global warming (Rose, 2005). A closed population of winter flounder that relies solely on an estuary as a spawning and nursery ground will likely exhibit poor recruitment, if that estuary has been degraded by human activities. Homing to spawning grounds by adults may be unfavorable when conditions do not inhibit the act of spawning but do diminish the survival of eggs and larvae (Harden Jones, 1968). Harden Jones (1968) also concluded that strict natal homing was not a sustainable life history strategy and that diverse migration behaviors are needed for a population to persist in a changing environment.

Divergent migrations impart resilience to populations against spatial variability in mortality (Secor, 1999). Passive telemetry revealed that winter flounder in the southern Gulf of Maine exhibit spatial heterogeneity in their use of spawning habitat and that coastal spawning was prevalent. Compared to estuarine spawning, coastal spawning likely leads to a greater dispersal of larvae. Therefore, a single coastal spawning contingent may provide a larval source for one or more estuarine nursery grounds. Coastal spawning contingents may confer resilience in a regional population during periods when estuarine productivity is low.

Our results indicate that coastal waters may provide essential spawning habitats for winter flounder in the Gulf of Maine. However, future research is needed to identify the prevalence of coastal spawning in other regions of the Gulf of Maine. Acoustic telemetry is a promising tool for conducting this research. For example, receiver gates could be placed across the mouths of estuaries along the coast, in a design similar to the one proposed by Grotheus and Able (2007). Ichthyoplankton studies could also be used to compare the densities of winter flounder eggs in estuarine and coastal waters. High-resolution trawl surveys could be used to sample the reproductive condition of winter flounder throughout the Gulf of Maine. Finally, coupled biophysical models would allow an examination of the dispersal of coastal spawned larvae in the Gulf of Maine.

Seasonal distribution of winter flounder

Bigelow and Schroeder (1953) and McCracken (1963) observed that flounder north of Cape Cod are more abundant in deeper, coastal waters during the winter months. Our observations in one region of the Gulf of Maine support this claim because only 10% of tagged of winter flounder at large during the winter months were detected within the shallow waters of the Plymouth estuary. Contrary to our observations, Howe and Coates (1975) claimed that flounder in the Gulf of Maine moved farther inshore into estuaries during the winter months. However, their analysis may have been hampered by a lack of tag returns during the fall and winter months.

Winter flounder in Newfoundland are thought to move to deeper coastal waters during the winter to avoid ice formation and extreme turbulence during storm events (Van Guelpen and Davis, 1979). Winter flounder may

[5] Marine Research, Inc. 1986. Winter flounder early life history studies related to the operation of Pilgrim Station—A review 1975–1984. Pilgrim Nuclear Power Station Environmental Monitoring Program – Report Series No. 2, 111 p. Boston Edison Company, Boston, MA.

also migrate to deeper waters during the winter to prevent their blood serum from freezing, which occurs between –1.25 and –1.38°C (Fletcher, 1977). Temperatures in the Plymouth estuary dropped to as low as –1.55°C during the winter of 2008, whereas the minimum recorded temperature in Plymouth Bay was 1.2°C. Therefore, the deeper waters of Plymouth Bay may act as a refuge from the extreme cold temperatures and ice formation that are present in the Plymouth estuary during the winter.

Tagged winter flounder were most commonly present in the estuary during the late spring, when water temperatures ranged from 9° to 16°C, which is within the preferred temperature range (12–15°C) of this species (McCracken, 1963; Reynolds, 1977). Although winter flounder were common in the estuary during the late spring, the majority of the tagged winter flounder remained in coastal waters during this period. Howe and Coates (1975) also reported that winter flounder are concentrated in shoal areas during the spring months. Although we were unable to capture adult winter flounder in the estuary from March through early May 2008, we cannot conclude that winter flounder were not present in the estuary during this time. Winter flounder in spawning condition often cease feeding or reduce their food intake (NMFS, 1999) and therefore it is less likely that we would have captured flounder using hook-and-line gear during the spawning season. In addition, flounder that were buried in the sediment may not have been available to the small trawl net that we were using to capture flounder in the estuary.

The emigration of winter flounder from the estuary coincided with rising temperatures at the onset of summer. Between 30 May and 19 June 2008 the majority of tagged winter flounder emigrated from the estuary as water temperature increased from 10° to 15°C (Fig. 6). These observations were consistent with previous reports that revealed that winter flounder will migrate to cooler waters when temperatures exceed 15°C (Bigelow and Schroeder, 1953; McCracken, 1963). Perlmutter (1947) found that the movements of winter flounder north of Cape Cod are typically localized, and Howe and Coates (1975) calculated that the average displacement of winter flounder tagged in Plymouth Bay was only 3 km. They also found that in the Gulf of Maine, winter flounder could find suitable temperatures (between 12° and 17°C) within 2 km of the shore zone during the summer. Weekly averaged temperatures in Plymouth Bay only exceeded 15°C twice in 2008, and did not exceed 15°C in 2009. Therefore, winter flounder leaving the Plymouth estuary were not forced to migrate long distances to reach suitable temperatures.

During the autumn months of 2008 five tagged individuals returned to the estuary as water temperatures decreased below their seasonal maxima. Bigelow and Schroeder (1953) also noted that winter flounder will return to the Plymouth estuary during the autumn months when temperatures start to cool.

Conclusions

By collecting large amounts of high-resolution data, we are able to offer insight into the fine-scale behavior and distribution of winter flounder in the southern Gulf of Maine. Our results indicate that winter flounder exhibit divergent spawning behaviors which support inferences of contingent structure and that coastal waters may provide essential spawning grounds for this species. As such, coastal waters should merit consideration in the assignment of Essential Fish Habitat for this species in the Gulf of Maine. In this region of the Gulf of Maine, estuarine residence appears to be brief, and dependent upon water temperature.

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Demographic characteristics of exploited tropical lutjanids: a comparative analysis

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Abstract—Demographic parameters from seven exploited coral reef lutjanid species were compared as a case study of the implications of intrafamily variation in life histories for multispecies harvest management. Modal lengths varied by 4 cm among four species (*Lutjanus fulviflamma*, *L. vitta*, *L. carponotatus*, *L. adetii*), which were at least 6 cm smaller than the modal lengths of the largest species (*L. gibbus*, *Symphorus nematophorus*, *Aprion virescens*). Modal ages, indicating ages of full selection to fishing gear, were 10 years or less for all species, but maximum ages ranged from 12 (*L. gibbus*) to 36 years (*S. nematophorus*). Each species had a unique growth pattern, with differences in length-at-age and mean asymptotic fork length (L_∞), but smaller species generally grew fast during the first 1–2 years of life and larger species grew more slowly over a longer period. Total mortality rates varied among species; *L. gibbus* had the highest mortality and *L. fulviflamma*, the lowest mortality. The variability in life history strategies of these tropical lutjanids makes generalizations about lutjanid life histories difficult, but the fact that all seven had characteristics that would make them particularly vulnerable to fishing indicates that harvest of tropical lutjanids should be managed with caution.

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Knowledge of the life history characteristics of an exploited species can help elucidate inherent resilience to anthropogenic effects such as fishing (Parent and Schriml, 1995; Jennings et al., 1998; Musick et al., 2000). Interspecific variation in life history characteristics may indicate that some species are more susceptible to overfishing than others. Life history characteristics vary widely among families of coral reef fish (Sale, 1991; Gust et al., 2002)—a feature particularly evident within the Lutjanidae. Some lutjanid species grow to sizes in excess of 1 m (e.g., cubera snapper [*Lutjanus cyanopterus*], red snapper [*L. sebae*]) and others reach smaller maximum sizes of less than 30 cm (e.g., two-spot banded snapper [*L. biguttatus*], bluestriped snapper [*L. notatus*]). Variable life spans and spatial distributions also have been recorded within the family. Lutjanids are typically gonochoristic (i.e., do not change sex) and often exhibit sex specific variation in life history traits (Polovina and Ralston, 1987). A high degree of variation in life history strategies among reef fish species within a family would suggest it is inappropriate to apply the same management strategy to all those species. Here we consider the lutjanids as a case study.

The Lutjanidae comprises approximately 103 species with a wide array of size and body form, making it one of the largest and most diverse families of fish (Carpenter and Niem, 2001). Lutjanids are found in tropical waters around the globe and are often associated with reef habitats (Carpenter and Niem, 2001). Lutjanids are of high commercial value throughout the world and are taken regularly in artisanal, recreational, and commercial fisheries (Newman et al., 1996; Kaunda-Arara and Ntiba, 1997; Marriott et al., 2007; Amezcua et al., 2006). The propensity of lutjanids to aggregate, particularly for spawning, and their predictably reef-associated distribution, make them potentially susceptible to overfishing. Concerns have been raised about the level of harvest and sustainability of fishing for lutjanid populations in some regions (Kamukuru et al., 2005; Amezcua et al., 2006).

Little is known about the specific spatial distribution and demograph-

ic characteristics of many lutjanid species (but see Newman et al., 1996, 2000a; Kaunda-Arara and Ntiba, 1997; Kritzer, 2002, 2004; Amezcua et al., 2006; Marriott et al., 2007). Many species remain unstudied and comparisons among species are few, even though research has covered much of the family's geographic range. including Mexico (Arreguín-Sánchez and Manickchand-Heileman, 1998; Amezcua et al., 2006), Kenya (Kaunda-Arara and Ntiba, 1997), the United States (Wilson and Nieland, 2001; Meyer et al., 2007), Japan (Shimose and Tachihara, 2005), the Great Barrier Reef (Newman et al., 1996, 2000a; Marriott et al., 2007), Arabian Gulf (Grandcourt et al., 2006), and the Indian Ocean (Newman and Dunk, 2003; Pilling et al., 2000). The few data that do exist indicate that at least some lutjanid species are long lived with life spans over 30 years (Newman et al., 1996; Wilson and Nieland, 2001; Newman and Dunk, 2003; Marriott et al., 2007).

In this study we compared the demographic characteristics of seven lutjanid species on mid and outer shelf reefs of the Great Barrier Reef (GBR), Australia, as a case study of the implications for intrafamily demographic diversity for managing multispecies fisheries. The species examined included the following: chinamanfish [*Symphorus nematophorus*]; green jobfish [*Aprion virescens*]; dory snapper [*Lutjanus fulviflamma*]; yellow-banded snapper [*L. adetii*]; humpback red snapper [*L. gibbus*]; brownstripe red snapper [*L. vitta*]; and spanish flag snapper [*L. carponotatus*]. These species are among the most common lutjanids caught on the GBR after the highly valued red snappers (*L. erythropterus, L. malabaricus, L. sebae*) (Newman et al., 2000b).

Demographic characteristics examined for each species included size, age, growth, mortality, and sex-specific patterns. Demographic parameters were compared to quantify differences in life history strategies among species and to infer the likely resilience of each species to fishing impacts. This information was used to assess whether common management measures would be appropriate across species within the lutjanid family. Such descriptive field studies also can be useful for providing the data sets to be used in meta-analyses for further developing our collective understanding of life history theory (e.g., Roff, 1984; Molloy et al., 2007). In this study we describe different aspects of biology across these closely related species. Samples from the same shallow coral reef habitats allowed us to control for taxonomic, geographic, and environmental effects to provide insight into the similarities or differences in life history strategies and thus theoretical trade-offs in evolved traits for moderate-size gonochoristic teleosts.

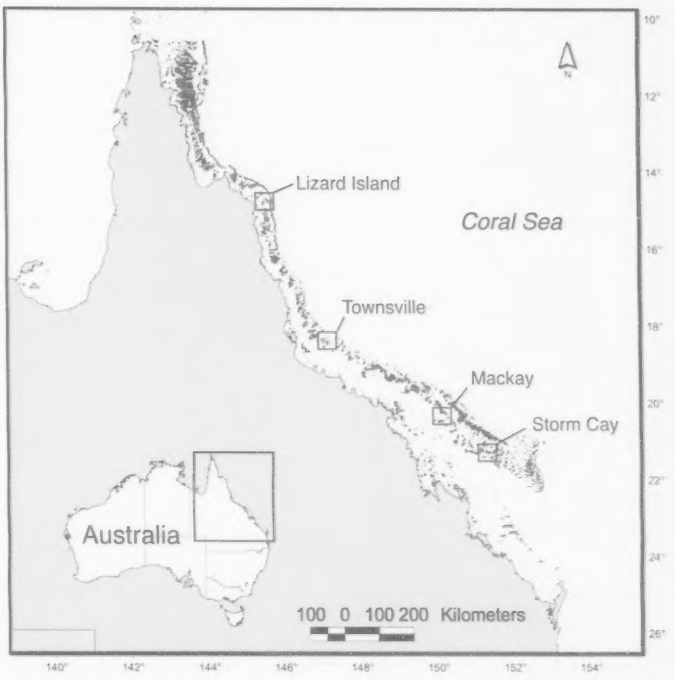

Figure 1

Map of the Great Barrier Reef region off the east coast of Australia showing the four sampling regions where lutjanids were collected for use in this study.

Materials and methods

Sample collection

Individuals of the seven lutjanids considered here were collected during the effects of line fishing (ELF) experiment[1] (Campbell et al., 2001) between 1995 and 2005 from four regions of the GBR spanning 7° of latitude: Lizard Island, 14°S; Townsville, 18°S; Mackay, 20°S; and Storm Cay, 21°S (Fig. 1). All fishing was done by handline with the same gear as that used in the operational commercial fishery, but survey effort was stratified to ensure roughly equal distribution around each reef and over two depth strata (above 12 m and below 15 m). Otoliths (sagittae) and gonads of fish were either dissected on the day of capture and processed as described below or fish heads were removed from filleted fish carcasses in the field, frozen, and otoliths were dissected upon return to the laboratory. Otoliths of five of the seven species were examined for age analysis (*A. virescens, S. nema-*

[1] Mapstone, B.D., C. R. Davies, L. R. Little, A. E. Punt, A. D. M. Smith, F. Pantus, D. C. Lou, A. J. Williams, A. Jones, A. M. Ayling, G. R. Russ, and A. D. McDonald. 2004. The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. CRC Reef Research Centre Technical Report no 52, 205 p. CRC Reef Research Centre, Townsville, Australia.

tophorus, L. carponotatus, L. gibbus, L. fulviflamma). Sufficient specimens were collected for comparisons among regions for only one species (*L. carponotatus*) and specimens for all other species were pooled across regions and years for analyses.

Fish processing

All fish were measured to the nearest millimeter fork length (FL) and weighed to the nearest gram before dissection. Otoliths were dissected from a subsample of specimens, cleaned, and stored dry in paper envelopes. Otoliths were embedded in epoxy resin and cut transversely through the primordium with a diamond-tipped blade on a low-speed saw to produce a thin section of 300–400 μm. Sections were mounted on glass slides by using Crystalbond adhesive (Aremco Products Inc., New York). Otoliths were read under reflected light at 40× magnification and opaque growth increments were counted from the primordium to the proximal (*in situ*) margin along the ventral ridge of the sulcus acousticus. Sectioned otoliths were read by one or more individuals. Where more than one reader was used, otoliths were read at least once by each of two independent readers and the age was accepted if these first two counts agreed. A third count was made by one of the two readers if the first two counts did not agree and a match between this third count and either of the previous two was accepted as the age of the fish or, if the third count did not match either of the first two counts, the median count was assigned as a final age estimate. The remaining otoliths were read by a single, experienced reader who counted each otolith at least twice with a minimum of 24 hours between consecutive counts. If the first two counts did not agree, a third count was completed to assign a final age through count agreement or to assign a median age, as described above.

Opaque increments were assumed to be annuli for the five species examined. Supportive evidence for annual periodicity in opaque increment deposition in otoliths has been demonstrated for the majority of tropical reef fish (Fowler, 1995; Choat and Robertson, 2002), lutjanids (e.g., Cappo et al., 2000), and for most of the study species: *L. vitta* (Davis and West, 1992; Newman et al., 2000a), *L. carponotatus* (Newman et al., 2000a; Kritzer, 2002), *L. adetii* (Newman et al., 1996), *L. fulviflamma* (Grandcourt et al., 2006), and *A. virescens* (Pilling et al., 2000). Age estimates derived from the otoliths for *L. gibbus* and *S. nematophorus* have not been validated hitherto, but we assumed that increment deposition also occurs on an annual basis for these species, as has been demonstrated for the majority of other tropical lutjanids. A violation of this assumption is likely to result in biases in the parameter estimates we present, such as for the von Bertalanffy parameter K and the instantaneous total mortality coefficient, Z. The magnitude of bias would likely inflate estimates for older-age species, and these estimates would vary among parameters, with a likely smaller influence on estimates of L_∞ (mean asymptotic fork length) (Choat et al., 2009). Gonads were examined to define the sex and maturity of individuals, but low sample sizes prevented meaningful analysis of detailed histological staging or gonadosomatic index analyses. Gonads were dissected and either frozen or preserved in FAACC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%) or 10% buffered formalin immediately after removal. Tissues were preserved in FAACC before May 1999 and 10% buffered formalin thereafter. The sex and maturity of *L. carponotatus* was established by macroscopic methods (Kritzer, 2004). The sex and maturity for a subset of individuals of other species were further assessed by histological analysis. Transverse histological sections were taken from the medial region of all gonads after the procedures outlined by Adams (2003). Female maturity was determined by the presence of vitellogenic oocytes, and the presence of brown bodies, atretic oocytes, vascularization, and the relative thickness of the gonad wall, all of which may indicate prior spawning (Sadovy and Shapiro, 1987; Ferreira, 1995; Adams, 2003). Male maturity was determined by the presence of sperm in the sperm sinuses.

Estimation of demographic parameters

Length- and age-frequency distributions were constructed from pooled samples and compared among species qualitatively. Differences in length and age frequencies by sex were assessed by using two-sample Kolmogorov-Smirnov tests where the largest of absolute discrepancies between relative cumulative frequency distributions (d_{max}) was compared with an approximate two-tailed critical value (D: Sokal and Rohlf, 1995). Growth was modeled with the von Bertalanffy growth function (VBGF) fitted by using a nonlinear least-squares regression of FL on age. The form of the VBGF was

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right),$$

where L_t = the length at age t;
L_∞ = the mean asymptotic fork length;
K = the growth coefficient or rate at which L_∞ is approached; and
t_0 = theoretical age at zero length.

The VBGF model was fitted to L_t on t data groups where t_0 was either constrained to zero (t_0=0) or unconstrained (estimated). This was done to examine the effects of the absence of smaller individuals in the sample and (for t_0 = 0) to allow biologically sensible comparisons of growth among species if lengths at age of younger fish (not sampled) extrapolated by the model were biologically unrealistic. VBGFs for *L. carponotatus* for all regions were compared by likelihood ratio tests.

Analysis of covariance (ANCOVA) was used to compare log-transformed length data from individuals across a common age range (5–12 years) among the five species with age as a covariate. A Tukey's *post hoc* test (P=0.05) was used to test for differences among species when a significant difference among the groups was detected by the ANCOVA.

Age-based catch curves (Ricker, 1975) were used to estimate the instantaneous rate of total mortality (Z) for each species. The natural log-transformed number of fish in each age class was regressed against the corresponding age on the descending slope of the age-frequency distribution to provide an estimate of total mortality, Z. Regressions were fitted from the first modal age class, presumed to be the first age class fully selected by the sampling gear, through the oldest age class that was preceded by no more than two consecutive zero frequencies. An ANCOVA was used to determine whether there were differences in mortality among regions for *L. carponotatus*. Z also was estimated by using the Hoenig (1983) estimator for fish populations from $\log_e Z = 1.46 - 1.01 \log_e t_{max}$, where t_{max} was the maximum observed age in years.

Sex ratios and size- and age-frequency distributions were examined to describe sex-specific aspects of population structure. Departure from a 1:1 sex ratio was tested with a chi-squared test by using Yates's correction for continuity (Zar, 1999).

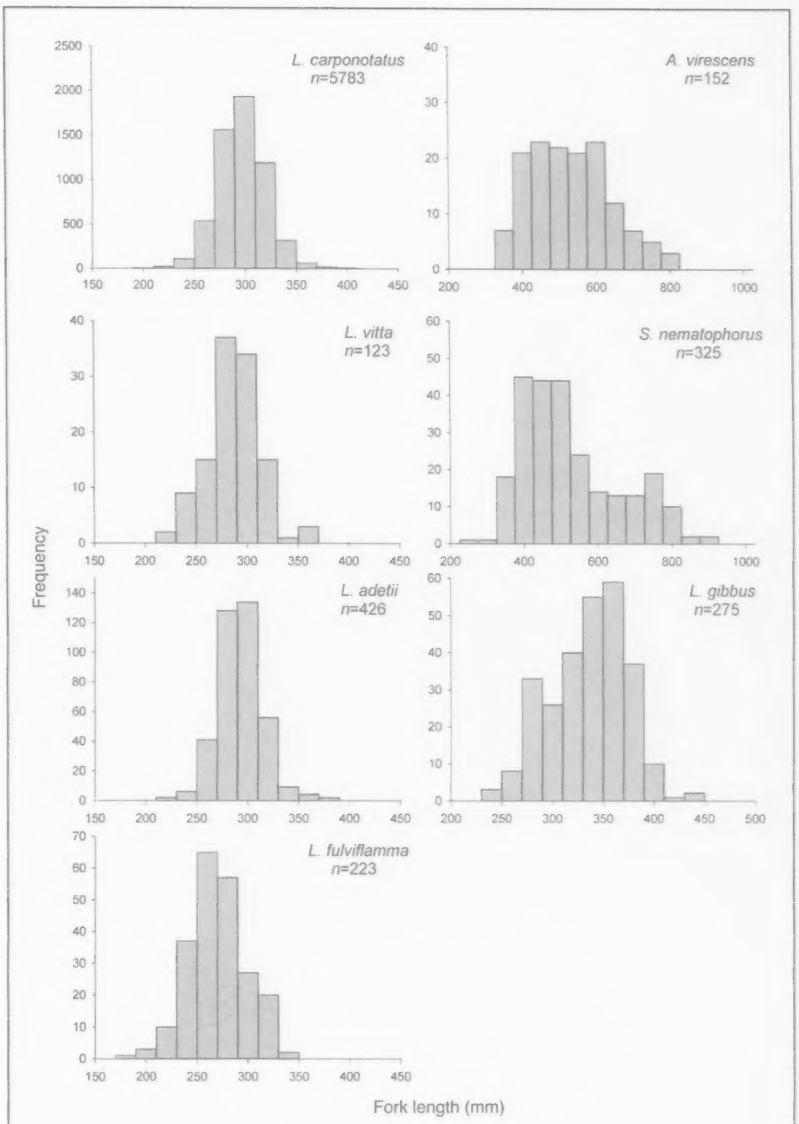

Figure 2

Length-frequency distributions for seven lutjanid species on the Great Barrier Reef between 1995 and 2005 (note difference in y axes).

Results

A total of 7307 individuals of the seven lutjanid species were sampled, of which *L. carponotatus* was the most abundant. The modal length in the sampled distributions differed among species (Fig. 2) and was largest for *S. nematophorus* (400–449 mm FL) and *A. virescens* (450–499 and 600–649 mm FL) and smallest for *L. fulviflamma* (260–279 mm FL). *Symphorus nematophorus* and *A. virescens* had the largest maximum fork lengths of 885 mm and 810 mm FL, respectively. Of the seven species, the sampled length ranges of *L. carponotatus*, *L. fulviflamma*, and *L. adetii* were most similar, with 72%, 89%, and 81% coming from the size range of 200–300 mm FL, respectively.

Age-frequency distributions varied considerably among the five species for which age was estimated. The modal age in the catch was 2 years for *A. virescens*, 3 years for *S. nematophorus*, 7 years for *L. carponotatus*, 8 years for *L. gibbus*, and 10 years for *L. fulviflamma* (Fig. 3). The catch of the two largest species (*S. nematophorus* and *A. virescens*) consisted predominately of younger age classes (<6 yr), whereas the catch of smaller species (*L. carponotatus*, *L. gibbus*, *L. fulviflamma*) included a higher proportion of fish sampled from older age classes (>8 yr; Fig. 3). The maximum age in the catch also

differed among species (Fig. 3) and the oldest fish was a 36-year-old *S. nematophorus*.

Regional and sex-specific differences in length- and age-frequency distributions could only be analyzed for *L. carponotatus* because of low sample sizes for all other species. There was a significant effect of sex on lengths (Kolmogorov-Smirnov test: n_1=1279, n_2=399, d_{max}=0.336, D=0.078, P<0.05) and ages (n_1=1279, n_2=399, d_{max}=0.281, D=0.078, P<0.05) for the frequency distributions and a greater proportion of males than females in the larger size classes and younger age classes (Fig. 4). Differences in growth by sex were significantly different (χ^2=68.34, P<0.0001), with males reaching a significantly greater maximum size than females (female: L_∞=278, K=0.43, t_0=–2.55; male: L_∞=293, K=0.55, t_0=–1.43).

The unconstrained fits of the VBGF differed substantially among species with *L. carponotatus*, *A. virescens*, and *L. fulviflamma* reaching a maximum size relatively early in life (Fig. 5). *Symphorus nematophorus* reached a maximum size somewhat later in life, and the growth curve for *L. gibbus* was not asymptotic. The lack of juvenile fish collected for all species, but particularly for *L. carponotatus*, *L. fulviflamma*, and *L. gibbus*, resulted in relatively flat fits of the unconstrained VBGF. The nonasymptotic growth pattern for *L. gibbus* indicates that under-sampling of larger individuals may also have occurred. VBGF parameter estimates for all species from the unconstrained fit are likely to be biased and should be interpreted with some caution.

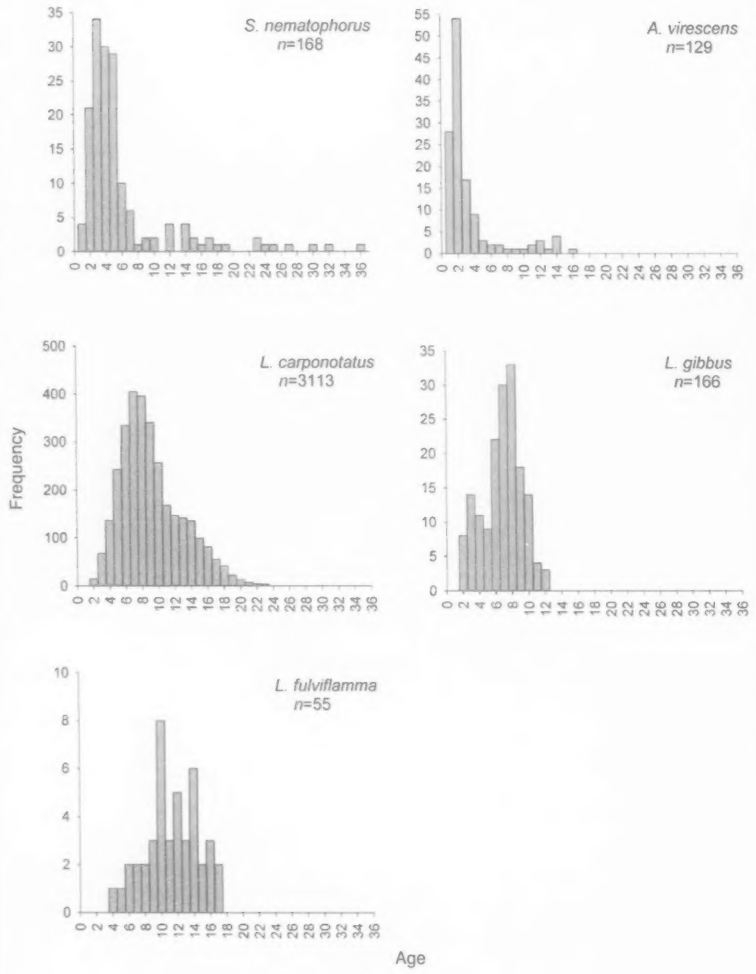

Figure 3

Age-frequency distributions for five lutjanid species on the Great Barrier Reef between 1995 and 2005 (note difference in *y* axes).

Constraining the VBGF by setting t_0=0 produced similar estimates of K and L_∞ to those for the unconstrained estimates for *L. carponotatus* and *L. fulviflamma*. Despite limited sampling of the youngest individuals, this similarity indicates that a sufficiently wide range of age classes were sampled in these populations to produce biologically reasonable estimates of growth without the need to constrain t_0. Constraining t_0 resulted in faster initial growth estimates (greater estimate of K) and smaller asymptotic length (L_∞) than the unconstrained fits for *S. nematophorus*, *A. virescens*, and *L. gibbus*. The constrained fit produced a more asymptotic growth curve for *L. gibbus*, indicating that constraining t_0 may have provided a more biologically realistic estimate of length-at-age for this species.

Both constrained and unconstrained growth curves differed across species. These species showed distinct differences in the rate of growth at young ages and the age at which they reached average maximum length: smaller species grew fast in the first couple of years and reached asymptotic length early, whereas larger species grew slightly slower in the first few years to reach an asymptotic FL later. The lack of small-size individuals resulted

in a lack of definition of early growth in the unconstrained curves when compared to constrained estimates. Both constrained and unconstrained growth curves for *L. carponotatus* and *L. fulviflamma* were relatively "square-shaped" (Choat and Robertson, 2002), revealing little growth over most of their life spans. Several species had K values >0.30/yr, indicating rapid growth to maximum size at a young age.

Comparison of growth rate among 5–12 year olds revealed significant differences among species ($F_{4,2503}$=1543.8, P<0.0001). *Post hoc* tests indicated that each species had a unique growth rate. Examination of age at 50% L_∞ indicated some differences between constrained and unconstrained fits (Table 1), but in all cases, 50% of asymptotic length was reached at relatively young ages compared with estimated longevity, and only *L. gibbus* took longer than 10% of expected longevity to reach 50% of asymptotic size (Table 1).

Lutjanus carponotatus was the only species with a sample size sufficient for regional analysis of growth data. Likelihood ratio tests indicated that patterns of growth differed significantly between Lizard Island, Mackay, and Storm Cay regions (χ^2=68.34, P<0.001) but there were similar L_∞ values among regions, and quite variable K values (Table 1). The most notable difference was the greater L_∞ (and lower K) in the Storm Cay region (Table 1).

Total mortality (Z) estimates calculated from catch curves varied significantly among the five species examined ($F_{4,41}$=5.61, P=0.001) (Fig. 6). Z was highest for *L. gibbus* and *A. virescens* and lowest for *L. fulviflamma* (Table 2). Mortality rates calculated by the Hoenig method resulted in more homogeneous estimates, of which highest rates were for *L. gibbus* and lowest for *S. nematophorus*. Mortality estimates calculated from catch curves were higher than those estimated by Hoenig's method for all species except *L. fulviflamma* (Table 2). Z for *L. carponotatus* did not vary significantly among the three regions ($F_{2,29}$=2.24, P=0.15) and therefore a single catch curve was fitted to data pooled across regions.

All except one of the individuals sampled (282-mm *L. gibbus*) were sexually mature, making analysis of size and age at maturity impossible. Adult sex ratios in a few of the sampled populations differed from a 1:1 sex ratio (Table 3), despite the expected gonochoristic nature of these species. Sex ratios of *L. carponotatus*, *L. gibbus*, and *L. vitta* were biased significantly toward males.

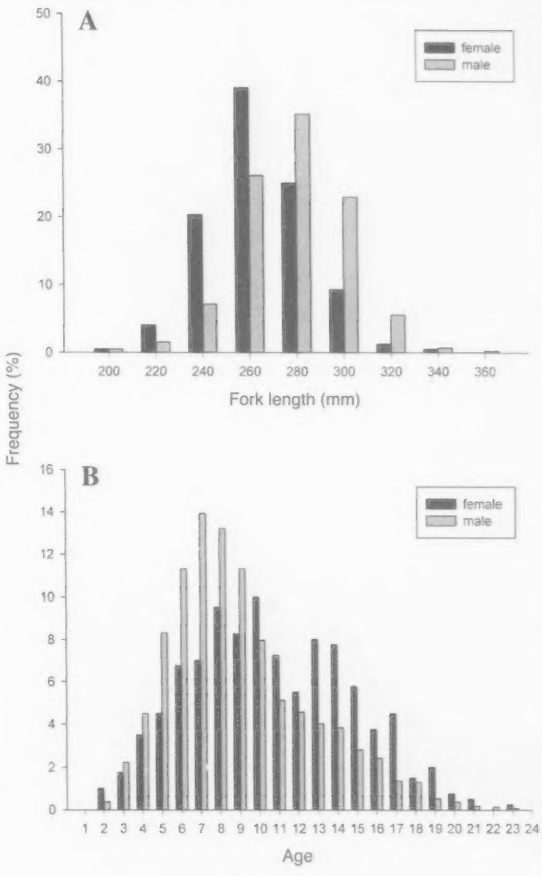

Figure 4

Sex-specific (**A**) length and (**B**) age frequency of *L. carponotatus* collected from the Great Barrier Reef from 1995 to 2005.

Discussion

Many coral reef fish species have overlapping spatial distributions, are found in similar habitats, and grow to roughly similar sizes. It might be expected that superficially similar species from the same family would have similar demographic characteristics and life history strategies. The results of this case study of lutjanid species, however, indicate that it is impossible to make generalizations about the life histories of members of a family, even where they grow to similar sizes and coexist in the same habitats. Even this small subset of seven lutjanid species had quite different growth, mortality, and longevity characteristics. Our results support previous findings for individual species but also provide evidence of the considerable differences among species in this family and highlight the need for careful, and potentially species-specific, approaches to managing the harvest of lutjanid assemblages.

Demographic characteristics of the lutjanid species described here must be considered in the context of the limitations of size selectivity of the fishing gear used to sample populations. No individuals below 200 mm FL were collected for any species, meaning the youngest age classes were not fully selected, resulting

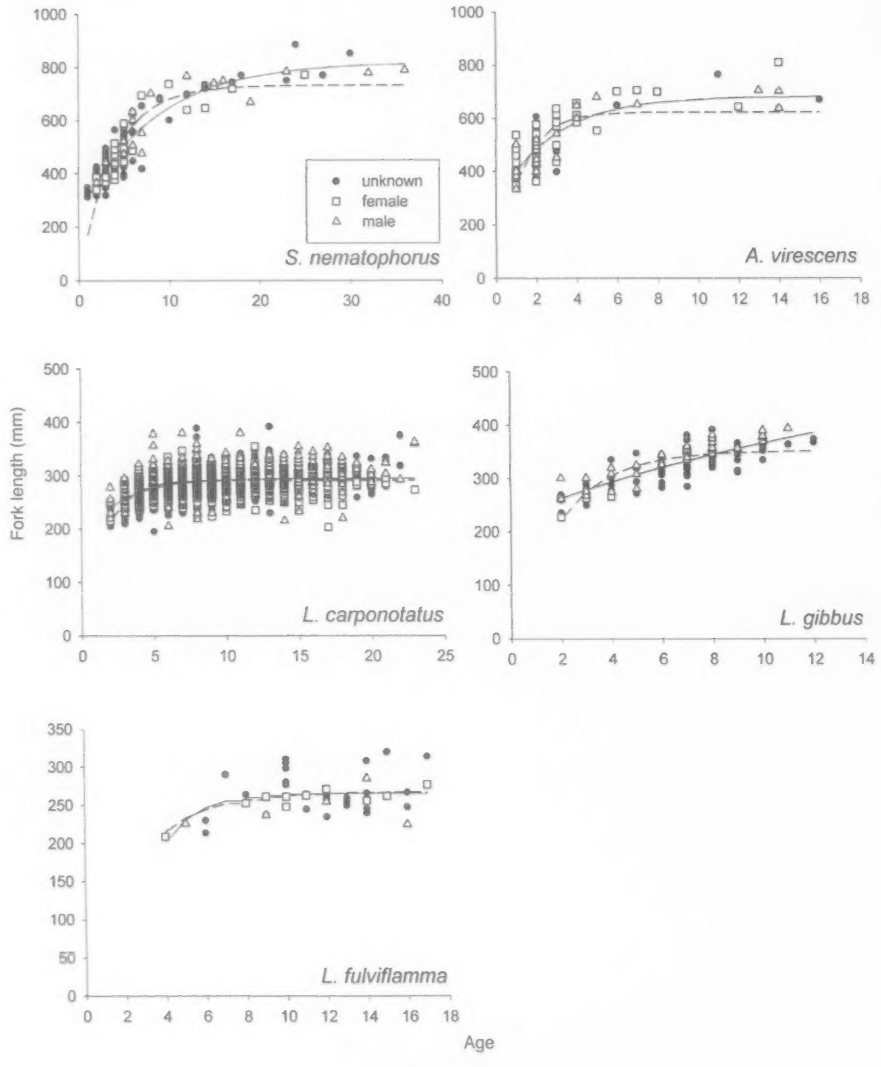

Figure 5

Length-at-age data and fitted von Bertalanffy growth function (VBGF) curves for five lutjanid species from the Great Barrier Reef between 1995 and 2005. Solid lines indicate unconstrained VBGF estimates and dashed lines indicate constrained (t_0=0) VBGF estimates.

in an absence of immature individuals for all, but one species. However, some individuals of most species were sampled in their first or second year indicating that these species mature at a very early age. The fact that full recruitment to the gear occurred at age 2 for *S. nematophorus* and at age 3 for *A. virescens*, the largest species sampled, illustrated the rapid early growth characteristic of many lutjanid species (Newman et al., 1996, 2000a; Kritzer, 2004; Grandcourt et al., 2006). It is important to note that the same sampling gear was used in this project as that most commonly used by commercial and recreational fisheries on the GBR and therefore the biological characteristics described here should reflect those characteristics of individuals of these species harvested by the fishery. Importantly, the sampled age distributions revealed the age range of these populations susceptible to fishing gear. It is also likely that many fish were not sampled because sampling was constrained to depths shallower than 30 m and to daylight hours, which are the most common

Table 1

Parameter estimates for the von Bertalanffy growth function parameters age at 50% L_∞ (mean asymptotic fork length) and percent longevity at 50% L_∞ for five lutjanid species from the Great Barrier Reef. K is the von Bertalanffy growth coefficient, and t_0 is the theoretical age at length zero. "U" indicates an unconstrained estimate, "C" indicates an estimate constrained by t_0=0. Region-specific growth curves for *L. carponotatus* were not constrained.

Species	L_∞ (mm)	K (/yr)	t_0 (yr)	Age (yr) at 50% L_∞	% longevity at 50% L_∞
S. nematophorus—U	820	0.12	–2.83	3	8.33
S. nematophorus—C	732	0.26	0	3	8.33
A. virescens—U	683	0.35	–1.53	0.5	3.13
A. virescens—C	623	0.85	0	1	6.25
L. gibbus—U	544	0.06	–9.48	2	16.67
L. gibbus—C	352	0.51	0	3	25.0
L. fulviflamma—U	265	0.61	1.66	1	5.88
L. fulviflamma—C	267	0.41	0	1	5.88
L. carponotatus—U	295	0.37	–2.58	0	0
L. carponotatus—C	291	0.66	0	1	4.35
L. carponotatus—Lizard Is	293	0.67	–0.17	—	—
L. carponotatus—Mackay	292	0.47	–1.68	—	—
L. carponotatus—Storm Cay	302	0.16	–9.35	—	—

Table 2

Estimates of mortality for five lutjanid species using catch curve and Hoenig (1983) estimators. Maximum age and age range used in mortality estimation are indicated.

Species	Maximum age (yr)	Age range (yr)	Catch curve Z (/yr) [SE]	Hoenig Z (/yr)
S. nematophorus	36	3–17	0.20 [0.05]	0.11
A. virescens	16	2–9	0.56 [0.07]	0.26
L. gibbus	12	8–12	0.63 [0.08]	0.35
L. carponotatus	23	7–23	0.30 [0.02]	0.18
L. fulviflamma	17	10–17	0.14 [0.06]	0.25

depth and time fished by commercial and recreational fishing crews. A small number of fishing crews fish during the night in deeper water (>50 m) where a greater proportion of larger lutjanids are caught (Marriott, personal commun.).

Limited sample sizes prevented the statistical analyses of sex- and region-specific variation in life history characteristics except for *L. carponotatus*. As with previous findings, *L. carponotatus* displayed sex-specific differences in these characteristics, with males reaching larger maximum sizes than females. Reasons for sex-specific size and age distributions may be due to a wide array of factors, including regional conditions and physiological costs of sperm and egg production. Kritzer (2004) also found male *L. carponotatus* to be larger than females and suggested that this is an Indo-Pacific trait within the lutjanids because it does not always occur in other geographic areas. Such sex-specific differences in lutjanid populations also may vary by region, although the magnitude of any sex-dependent variation within a geographic area remains poorly understood. Hence, our parameter estimates for the remaining species from samples pooled over regions of the GBR may not be as informative as we would like, but they nevertheless provide a good starting point for comparison and applicability to other regions where data remain scarce or absent.

Age and growth

Five of the seven species examined grew to similar sizes, but three of these demonstrated different longevities and the two largest species showed a twofold range in longevity for roughly similar maximum sizes, again illustrating the lack of a relationship between length and age across tropical lutjanids. High maximum ages

Table 3

Number and size of male and female lutjanid individuals sampled from the Great Barrier Reef between 1995 and 20o5 for reproductive analysis. Size range is included in parentheses; values in bold indicate significant difference from an even sex ratio.

	Female		Male		
Species	*n*	Mean size (mm FL)	*n*	Mean size (mm FL)	Sex ratio F/M
L. fulviflamma	28	263 (209–315)	16	250 (219–285)	1.75
S. nematophorus	32	533 (340–772)	41	485 (320–789)	0.78
A. virescens	50	511 (332–810)	32	509 (334–778)	1.56
L. adetii	18	284 (254–374)	22	290 (243–341)	0.82
L. gibbus	8	277 (227–356)	48	330 (262–418)	**0.17**
L. vitta	7	266 (204–307)	18	270 (226–310)	**0.39**
L. carponotatus	520	274 (203–355)	1722	292 (205–405)	**0.30**

of 36 and 23 years were evident in *S. nematophorus* (the largest species) and *L. carponotatus* (the second smallest species), respectively, despite their different maximum sizes. *Lutjanus gibbus*, *A. virescens*, and *L. fulviflamma* had shorter life spans and maximum ages of 12, 16, and 17 years, respectively. *Lutjanus carponotatus* have previously been reported to have maximum ages of 18 and 20 years (Newman et al., 2000a; Kritzer, 2002, 2004) which are consistent with the 23 year maximum obtained here. Shorter longevities recorded for *L. gibbus*, *A. virescens*, and *L. fulviflamma* align with those from other lutjanid species such as *L. vitta* (12 years, Newman et al., 2000a), *L. guttatus* (rose snapper, 11 years, Amezcua et al., 2006), and *L. fulviflamma* (14 years, Grandcourt et al., 2006). In contrast, *L. adetii*, a small species similar in size and appearance to *L. vitta*, has a reported maximum age of 24 years (Newman et al., 1996), further demonstrating the variability in life histories of similar size lutjanid species.

This and most previous studies reveal that these species have rapid initial growth despite differences in size and longevity; however, they reach asymptotic sizes at relatively young ages (Newman et al., 1996, 2000a; Kritzer, 2002, 2004; Grandcourt et al., 2006). Newman et al. (1996) suggested that size could not be used to infer age for *L. adetii* beyond five years of age. This principle is probably applicable for many lutjanid species and is supported by the growth patterns for four of the five species for which growth was analyzed, the exception being *L. gibbus*. All five species reached 50% of L_∞ before reaching 4 years of age. Caution should be used when generalizing, however, because red bass (*L. bohar*) and goldband snapper (*Pristipomoides multidens*) have been shown to be slow growing, long lived, and late maturing, showing a classic K-selected life history (Newman and Dunk, 2003; Marriott et al., 2007). That result contrasts with the fast growth observed in most other lutjanid species so far examined.

Lutjanus gibbus was the only species that did not reach an asymptote in the unconstrained growth curve. This may have been the result of the gear excluding smaller and younger individuals, a proposition supported by the fact that the constrained VBGF curves did produce an asymptote and the unconstrained functions produced an unrealistic t_0 value of –9.48. Observations that larger individuals were collected from deeper water indicate that the largest size and oldest age classes of *L. gibbus* and *S. nematophorus* may have been undersampled. Alternatively, these species may indeed have a long growth period and not stop growing throughout life, as does *L. bohar* (Marriott et al., 2007). The largest reported *L. gibbus*, however, was 50 cm total length (TL) (Carpenter and Niem, 2001)—only 5 cm larger than the largest individual sampled in this study (418 mm FL, ≈500 mm TL). *Lutjanus gibbus* was also the species with the highest mortality estimates from both catch curve and Hoenig's estimators, indicating that it had the highest turnover rates. Further sampling will be required to gain a better understanding of the age and growth characteristics of this species and resolve whether the differences in characteristics between *L. gibbus* and the other species examined were attributable to different life history strategies or to the effects of species-specific sampling biases.

All five species for which age was estimated reached 50% of the estimated L_∞ at young ages in relation to their maximum age. The percentage of longevity at which 50% L_∞ was reached was similar for most spe-

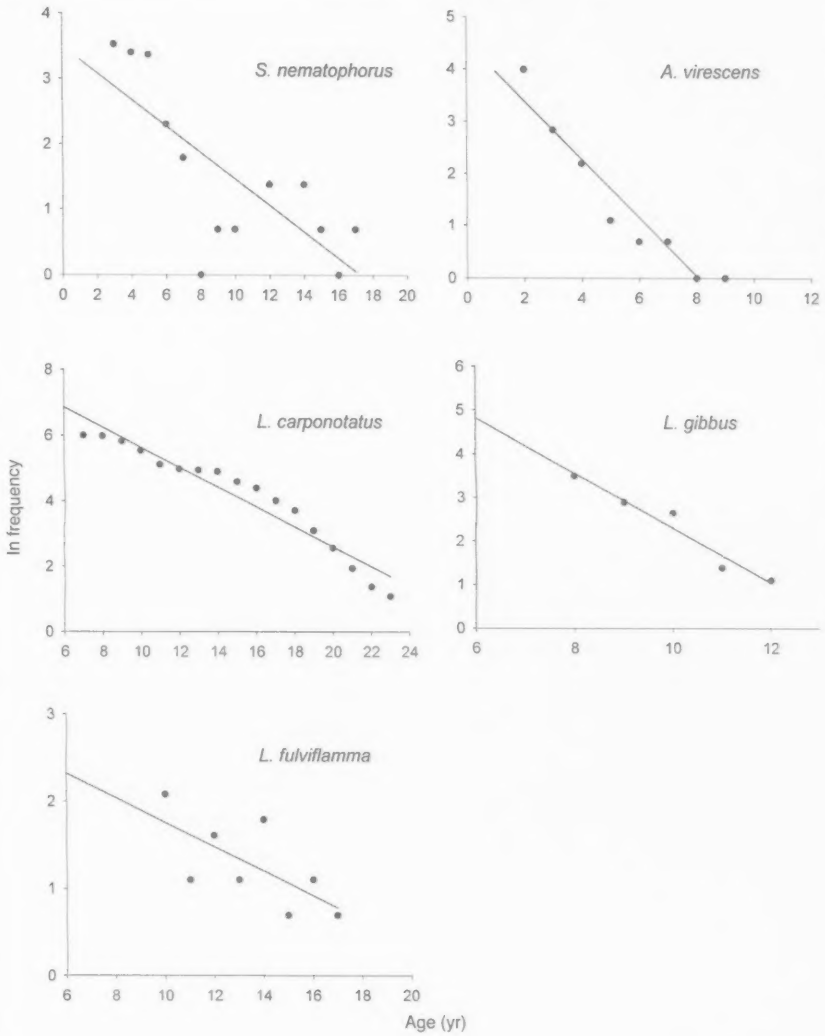

Figure 6

Catch curves for five lutjanid species from the Great Barrier Reef between 1995 and 2005. The slopes of the regressions provided estimates of the rate of total mortality (Z) for each species.

cies, and *L. gibbus* was the only species taking greater than 10% of its longevity to attain 50% L_∞. Growth of *L. carponotatus* varied significantly among regions spanning 7° latitude, growing more quickly to smaller asymptotic lengths in the more equatorial regions than in the south. Although statistically significant, the difference in growth may have little biological significance with L_∞ varying only about 3% among regions. Regional variation in growth for the other species remains unknown because of a lack of data but results for *L. carponotatus* reveal potential environmental influences on observed patterns for these other species.

Mortality

Estimates of mortality were likely biased because of selectivity of the sampling gear. For example, the positively skewed age distributions for *S. nematophorus* and *A. virescens* indicate that older fish were less available to the sampling gear and were likely to be under-

represented in the sample, resulting in overestimates of Z from catch curves. Estimates of Z derived from Hoenig's equation may be more appropriate for these species. Similarly, older individual *L. gibbus* and *L. fulviflamma* may not have been collected by the gear and if so, under-sampling may have resulted in overestimates of Z from the catch curves and Hoenig's method. Notwithstanding these potential biases, comparison of mortality rates revealed that *A. virescens* had a similar mortality rate to that of *L. gibbus*, indicating that *A. virescens* also has a relatively high population turnover rate. *Aprion virescens* grows quickly to a large size but may not live as long as other lutjanid species, despite attaining relatively large sizes. *Symphorus nematophorus*, for example, attained the largest size and had the second lowest mortality rate of the species examined. *Lutjanus fulviflamma* mortality estimates differed most between estimation methods, with catch curve estimates resulting in lowest mortality rates for this species (0.14/yr), but the Hoenig estimate revealed higher mortality rates (0.25/yr), similar to those for *A. virescens* and *L. gibbus*. The Hoenig estimate was also similar to rates previously reported for *L. fulviflamma* (0.29/yr, Grandcourt et al., 2006), indicating some bias in the estimate from catch curves. Like *L. gibbus*, *L. carponotatus* under six years of age could not be used in catch curve estimates of mortality, but the 6–23 year age classes yielded mortality estimates for *L. carponotatus* of 0.30/yr (catch curve) and 0.18/yr (Hoenig), similar to estimates calculated previously for this species (0.20/yr, Newman et al., 2000a; 0.26–0.29/yr, Kritzer, 2004). The range of mortality estimates for the species examined in this analysis agree well with those for other lutjanids (Newman et al., 1996, 2000a; Amezcua et al., 2006) and are another indication of the variability in life history strategies within the family.

Maturity and sex ratio

All except one individual sampled across all species were sexually mature, supporting the conclusion that these lutjanids reach sexual maturity early in life. Biased sex ratios were observed for all of the species sampled although the apparent biases were statistically significant for only three species. Two species (*L. fulviflamma*, *A. virescens*) showed large but nonsignificant female-biased sex ratios, whereas all others showed a male-biased ratio, and three (*L. carponatatus*, *L. vitta*, *L. gibbus*) were not significantly different from 1:1. Lutjanids are gonochoristic species and therefore it may be expected that adult sex ratios would be close to 1:1 in local populations, although at least three other studies have revealed biased sex ratios. Kritzer (2004) found that *L. carponotatus* had a female-biased sex ratio, whereas Newman et al. (2000a) reported a strongly male-biased sex ratio for the same species in similar locations to those that we examined. Studies of *L. fulviflamma* from different locations showed widely variable sex ratios. Kaunda-Arara and Ntiba (1997) reported a male-biased sex ratio in Kenya, and Grandcourt et al. (2006) reported a female-biased sex ratio in the southern Arabian Gulf. It is difficult, therefore, to establish generic patterns of sex ratios across, or even within, lutjanid species given the contradictory patterns in the literature and among the species sampled here. It is possible that sex-ratio bias is a result of a differential survival of males and females or sex-specific patterns in distribution that would result in males and females having different probabilities of capture in the sampling strategies used in various studies, including the present one. Kritzer (2004) was one of the few to have examined mortality by sex, but no difference in mortality by sex was found. This single result may indicate that differential spatial distributions may be a more likely cause of sex-ratio biases in samples of lutjanid populations. It has been suggested that sex ratio may be more even during spawning events (Kritzer, 2004), but no data are available to test this hypothesis.

Implications for management of lutjanid populations

An improved understanding of the demographic parameters of gonochoristic species is crucial to furthering research on the effects of fishing on their populations. Results here clearly demonstrate that all or even superficially similar (e.g., in size) subsets of lutjanid species should not be treated in the same manner in these types of analyses and that vulnerability is likely to be variable within the family. Careful consideration of the inherent life history variability of these species is required in the development of theories and generalizations about this family and others.

This case study of seven lutjanid species clearly indicates that data from one species cannot be applied to another in determining appropriate management measures for these populations. Some species appeared to be more susceptible than others to overexploitation by fisheries because of their longer life spans and lower rates of mortality. *Symphorus nematophorus* is a good example of a species with a long life span, large size, and low mortality. The combination of these factors could make this species a desirable fisheries target (owing to its larger size than other lutjanids), but also one of the most vulnerable because of its life history characteristics. *Symphorus nematophorus* and *L. gibbus* are currently no-take species within the GBR and have historically been avoided because of a potential risk of ciguatera (a form of food poisoning from eating large reef fish), and therefore these species are largely protected from harvest within this region, although this may not be the case in other parts of their range.

In comparison, the longevity of *L. carponotatus* and *L. adetii* in relation to other lutjanid species may make them more vulnerable to overfishing than sibling species (Newman et al., 1996). Despite their small size and fast growth, these populations may be more vulnerable than similar species such as *L. vitta* which have shorter longevities and hence potentially faster population turnover rates (Newman et al., 2000a). Notably, most of the species examined here recruited to the fishing gear at

relatively early ages but also apparently reached sexual maturity before recruitment to the fishery. The existence of early maturity in relation to longevity indicates a life history strategy with high reproductive potential in older individuals—perhaps indicative of adaption to low-frequency episodic recruitment successes (Kritzer, 2002, 2004). These characteristics may mean that lutjanids are particularly vulnerable to recruitment collapse from sustained harvest at relatively low rates of fishing-induced mortality.

Current management measures for lutjanid species within the GBR are precautionary to protect the widest possible range of lutjanid family members, but this may not be the case in other parts of their range and implications of differences among species should be considered in such situations. The presence of substantial variation in life histories among species would indicate that the data presented here could serve as a benchmark for these species in other regions, but should not be applied to different species that may not have comparable demographic parameters despite morphometric similarities to the species examined here. Failure to recognise differences in life histories when implementing management strategies across species may result in over-exploitation of some species, under-exploitation of others, or both. Furthermore, we recommend that local species-specific estimates of population parameters are obtained wherever possible because significant regional and local variation in population parameters is becoming increasingly apparent for tropical reef fish populations (e.g., Adams et al., 2000; Kritzer, 2002; Williams et al., 2003). Consequently, estimates derived from local populations are likely to significantly improve assessments and advice for the management of particular stocks.

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Asymmetric conservation benefits of circle hooks in multispecies billfish recreational fisheries: a synthesis of hook performance and analysis of blue marlin (*Makaira nigricans*) postrelease survival

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Abstract—We evaluated the conservation benefits of the use of circle hooks compared with standard J hooks in the recreational fishery for Atlantic istiophorid billfishes, noting hooking location and the presence of trauma (bleeding) for 123 blue marlin (*Makaira nigricans*), 272 white marlin (*Kajikia albida*), and 132 sailfish (*Istiophorus platypterus*) caught on natural baits rigged with one of the two hook types. In addition, we used pop-up satellite archival tags (PSATs) to follow the fate of 61 blue marlin caught on natural baits rigged with circle hooks or on a combination of artificial lure and natural bait rigged with J hooks. The frequencies of internal hooking locations and bleeding were significantly lower with circle hooks than with J hooks for each of the three species and were significantly reduced for blue marlin caught on J hooks than for white marlin and sailfish taken on the same hook type. Analysis of the data received from 59 PSATs (two tags released prematurely) indicated no mortalities among the 29 blue marlin caught on circle hooks and two mortalities among the 30 blue marlin caught on J hooks (6.7%). Collectively, the hook location and PSAT data revealed that blue marlin, like white marlin and sailfish, derive substantial conservation benefits from the use of circle hooks, and the negative impacts of J hooks are significantly reduced for blue marlin relative to the other two species.

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Istiophorid billfishes in the Atlantic Ocean experience considerable fishing pressure and most stocks are overfished. The greatest source of fishing-induced mortality for istiophorids results from the pelagic longline fishery that targets tunas and swordfish; however, artisanal and recreational fisheries also represent significant sources of mortality for some species (Arocha and Ortiz, 2006). The United States National Marine Fisheries Service (NMFS) manages the recreational billfish fishery with relatively large minimum sizes released to ensure that the majority of billfishes are released: 251 cm (99 in) lower jaw fork length (LJFL) for blue marlin (*Makaira nigricans*), 168 cm (66 in) LJFL for white marlin (*Kajikia albida*), and 152 cm (60 in) LJFL for sailfish (*Istiophorus platypterus*). No recreational landings are allowed for longbill spearfish (*Tetrapturus pfluegeri*), and no management measures currently exist for roundscale spearfish (*T. georgii*). As a result of these management measures and changes in angler behavior promoting live release of these species (Ditton and Stoll, 2003), the U.S. recreational billfish fisheries are primarily catch-and-release fisheries, and up to 99% of white marlin are released alive annually (Goodyear and Prince, 2003). However, not all billfishes that are released alive survive capture; postrelease mortality can be significant in some fisheries (Domeier et al., 2003; Horodysky and Graves, 2005).

A growing body of evidence indicates that the use of circle hooks can greatly reduce the incidences of internal (deep) hooking, hook induced trauma (bleeding), and postrelease mortality of piscivorous fishes (Muoneke and Childress, 1994; Skomal et al., 2002; Cooke and Suski, 2004), including billfishes (see Serafy et al., 2009). For istiophorid billfishes, live and dead natural baits rigged with J hooks reveal higher frequencies of internal hooking locations and trauma for sailfish, striped marlin (*K. audax*), and white marlin than the same baits rigged with circle hooks (Prince et al., 2002, 2007; Domeier et al., 2003; Horodysky and Graves, 2005). Using pop-up satellite archival tags (PSATs) to follow the fate of released fish, Domeier et al. (2003) noted a reduced but nonsignificant postrelease mortality for striped marlin caught on live natural baits rigged on circle hooks, and Horodysky and Graves (2005) reported a highly significant reduction

in postrelease mortality of fish caught on circle hooks compared to those caught on J hooks. In response to the depleted stock condition of Atlantic billfishes and the reduction in undesirable hooking locations and postrelease mortality resulting from the use of circle hooks, NMFS in 2008 implemented a management measure requiring the use of non-offset circle hooks in natural baits for all Atlantic billfish tournaments. During the rule-making process, NMFS received several comments stating that blue marlin have lower rates of deep hooking with J hooks than white marlin or sailfish, especially when caught on artificial lure and natural bait combinations rigged with J hooks, a common terminal tackle used in the Atlantic recreational fishery. It was also suggested that blue marlin released from the recreational fishery have high rates of survival.

Little is known about the effects of hook type on postrelease survival of blue marlin. A preliminary study on the use of PSATs to investigate postrelease survival of blue marlin inferred survival for at least eight of nine individuals caught on lures or skirted baits with J hooks trolled at relatively high speeds in the Bermuda recreational fishery (Graves et al., 2002). However, there were no data to directly compare the postrelease mortality of blue marlin caught on natural baits or on a combination of artificial lure and natural bait rigged with either circle hooks or J-hooks. To gain insights into the relative conservation benefits of circle hooks in the recreational fishery for Atlantic blue marlin and other istiophorids, we compiled data on hooking location and the incidence of trauma (bleeding) for 123 blue marlin, 272 white marlin, and 132 sailfish caught on natural baits rigged with either J hooks or circle hooks. Furthermore, to estimate the postrelease mortality of blue marlin caught on natural baits with circle hooks or artificial lure and natural bait combinations with J hooks, we deployed 61 PSATs to follow the fate of blue marlin caught on one of the two types of terminal tackle.

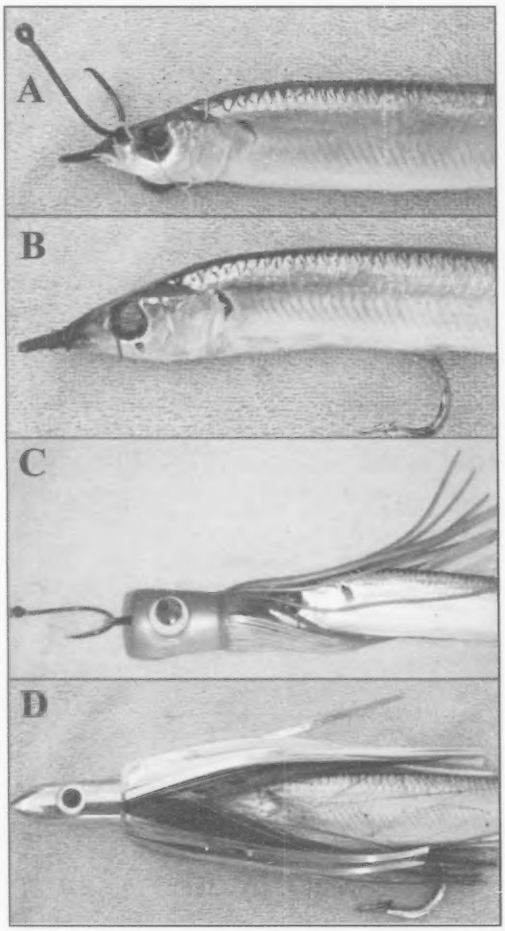

Figure 1

Bait and terminal tackle combinations used to investigate hooking location, presence or absence of trauma, and postrelease survival of western Atlantic istiophorid billfishes caught in the recreational fishery: (**A**) naked ballyhoo with circle hook; (**B**) naked ballyhoo with J hook; (**C**) artificial lure (chugger) and ballyhoo combination with circle hook; and (**D**) artificial lure (Ilander) and ballyhoo combination with J hook (photo by Ken Neill).

Materials and methods

Hooking location

Information on hook type, hooking location, and trauma (the presence of bleeding) was collected by the authors for all blue marlin, white marlin, and sailfish caught on trolled plain (naked) ballyhoo (*Hemiramphus brasiliensis*) baits during our PSAT tagging operations in the western North Atlantic from 2006 through 2009. Similar information was recorded by three cooperating charter captains (one from Oregon Inlet, NC, USA, and two from La Guaira, Venezuela) for billfishes caught during fishing operations in 2006. To accommodate captain and charter angler preferences, a variety of hook models and sizes were employed in the different fishing operations, but the most common J hook model was the Mustad 9175, size 7/0 (Mustad, Gjövik, Norway), and the most common circle hook model was the Eagle Claw L2004EWF, size 8/0 (Eagle Claw, Denver, CO). As is typical for this fishery, circle hooks were left exposed, rigged to the head of the bait, whereas J hooks were inserted through the mouth of the bait fish with the tip exiting the ventral surface (Fig. 1, A and B).

Baits were trolled at approximately 6 nm/hr (11.1 km/hr) during daylight hours on 30–50 lb (13.6–22.7 kg) class fishing tackle. As billfish approached the trolled bait, anglers would typically decrease tension on the line for periods of 4–10 s, "dropping back" the ballyhoo bait to the feeding billfish, which provided time for the

animal to ingest the bait before feeling tension on the line (see Jolley, 1974; Mather et al., 1975; Prince et al., 2007, for a description of this fishing method), although, in some instances the fish attacked trolled baits before an angler could reach the rod and drop back. The location of the hook and the presence or absence of bleeding (visible blood) was noted at the time of capture. Hooking locations were classified as external when all or part of the hook was visible outside of the fish's mouth, including fish that were foul hooked (hooked in areas away from the fish's mouth), and internal if no part of the hook was visible when the fish's mouth was closed.

Postrelease survival

PSATs were attached to 61 blue marlin caught in recreational fisheries in the western Atlantic Ocean. Fish were caught by using J hooks and circle hooks that were rigged with natural baits consisting of ballyhoo or Spanish mackerel (*Scomberomorous maculatus*). Baits were rigged in a manner typical for the fishery. J hooks were inserted inside the baits, which were fished in combination with a skirted artificial lure (e.g., Ilander [L & S Bait Company, Largo, FL], chugger [Mold Craft Lures, Pompano Beach, FL], or Seawitch [C & H Lures, Jacksonville, FL]) attached directly ahead of the bait (Fig. 1, C and D). Circle hooks were rigged externally on the baits, either on top of the head or directly in front of the bait. In some cases, a small artificial lure (chugger) was placed between the circle hook and the bait.

Blue marlin were caught on 30–130 lb (13.6–59.1 kg) class sportfishing tackle in waters off the United States mid-Atlantic coast; St. Thomas, U.S. Virgin Islands; Punta Cana, Dominican Republic; La Guaira, Venezuela; and Porto Seguro, Brazil, between September 2007 and October 2009 (Appendix 1). As is typical for the fishery, the vessel was maneuvered by the captain to assist the angler in the capture of the fish. Blue marlin were not brought alongside the vessel until they were considered to be sufficiently calm to allow accurate tag placement.

The first 61 fish available to us were tagged with a Microwave Telemetry PTT 100 HR tag (Microwave Telemetry, Inc., Columbia, MD), programmed for release after 10 days. This tag model records temperature, pressure (depth), and light levels approximately every 90–120 s. The tags were rigged as described in Graves et al. (2002), and deployed as described in Horodysky and Graves (2005). The location of the hook and presence or absence of bleeding was noted for each fish at the time of tagging. If practical, the hook was removed from the fish before its release. As is customary in this fishery, blue marlin that were unable to maintain their position upright in the water column were resuscitated by using the forward motion of the vessel to facilitate movement of water over the fish's gills before release (Appendix 1).

Survival of released blue marlin was inferred from temperature and depth profiles following the protocols of Horodysky and Graves (2005). Net displacement of each fish was calculated as the minimum straight line distance from the point of release to the point of tag pop-up. Cochran-Mantel-Haenszel (CMH) or Fisher's exact tests were used to address the effect of the J hooks and circle hooks on hooking location, hook-induced trauma, and survival. A Yates correction for small sample size was applied in conducting CMH tests when expected cell values were less than 5 (Agresti, 1990). All statistical analyses were conducted in the Statistical Analysis System, vers. 9.1 (SAS Institute, Cary, NC). Bootstrapping simulations were performed to determine the 95% confidence intervals of the estimates of mortality after release by using the software developed by Goodyear (2002).

Results

Hooking location

Hooking location and the presence or absence of bleeding were noted for 123 blue marlin, 272 white marlin, and 132 sailfish caught on natural baits rigged with either J hooks or circle hooks (Table 1). The incidence of internal hooking with J hooks ranged from 19.1% (blue marlin) to 44.4% (white marlin), and the frequency of internal hooking locations for fish caught on circle hooks was considerably lower, ranging from 1.8% (blue marlin) to 6.2% (sailfish). For blue marlin, white marlin, and sailfish, J hooks had a significantly higher probability of internal hooking locations than circle hooks ($P<0.007$, $P<0.0001$, $P<0.001$, respectively). The frequency of internal hooking locations for J hooks in blue marlin (19.1%) was less than half the value observed for white marlin and sailfish (44.4% and 41.2%, respectively), and the difference between blue marlin versus white marlin and sailfish combined was significant ($P<0.0014$).

The occurrence of trauma (bleeding) mirrored the pattern observed for internal hooking locations between the two hook types for each of the three billfishes. Across the three species, over 81% of the instances of bleeding (44/54) were associated with internal hooking locations (7/9 blue marlin, 20/24 white marlin, and 16/17 sailfish). Bleeding of fish caught on circle hooks ranged from 0% in blue marlin to 2.5% in sailfish (Table 1). For blue marlin, white marlin, and sailfish, J hooks had a significantly higher probability of inducing bleeding than circle hooks ($P<0.0141$, $P<0.001$, $P<0.0001$, respectively). As with the occurrence of internal hooking locations with J hooks among the three species, the frequency of bleeding observed in blue marlin (13.2%) was less than half that observed in white marlin and sailfish (both 33.3%); blue marlin had significantly lower rates of bleeding resulting from the use of J hooks than white marlin and sailfish combined ($P<0.027$).

Postrelease survival

Sixty-one blue marlin were caught on natural baits rigged with circle hooks (30) or on a combination of artificial lure and natural bait rigged with J hooks (31),

Table 1

Hooking location (frequency; 95% confidence interval) and presence or absence of trauma (bleeding, not bleeding) for observed recreational catches of blue marlin (*Makaira nigricans*, n=123), white marlin (*Kajikia albida*, n=272), and sailfish (*Istiophorus platypterus*, n=132), caught on natural baits rigged with either J hooks or circle hooks in the western North Atlantic Ocean.

Species / Hook type	Hook location		Trauma	
	Internal	External	Bleeding	Not bleeding
Blue marlin				
Circle	1 (1.8%; 0–5.4%)	54 (98.2%; 90.0–99.9%)	0 (0%; 0–2.0%)	55 (100%; 93.5–100%)
"J"	13 (19.1%; 10.6–28.5%)	55 (80.9%; 69.5–89.4%)	9 (13.2%; 6.2–23.6%)	59 (86.8%; 78.7–94.8%)
White marlin				
Circle	4 (2.0%; 0.6–5.0%)	196 (98.0%; 94.5–99.5%)	2 (1.0%; 0–2.4%)	198 (99.0%; 96.4–99.9%)
"J"	32 (44.4%; 32.7–56.6 %)	40 (55.6%; 43.4–67.3%)	24 (33.3% ; 22.4–44.2%)	48 (66.7%; 54.6–77.3%)
Sailfish				
Circle	5 (6.2%; 2.0–13.8%)	76 (93.8%; 86.0–97.8%)	2 (2.5%; 0.3–8.6%)	79 (97.5%; 91.4–99.7%)
"J"	21 (41.2%; 27.6–55.8%)	30 (58.8%; 44.3–72.4%)	17 (33.3%; 20.7–47.9%)	34 (66.7%; 52.1–79.2%)

tagged with Microwave Telemetry PSATs, and released. Three blue marlin were released off the U.S. mid-Atlantic coast; 26 off St. Thomas, U.S. Virgin Islands; 2 off Punta Cana, Dominican Republic; 21 off La Guaira, Venezuela, and 9 off Porto Seguro, Brazil (Appendix 1). Estimated fish weights ranged from 70 lb (31.8 kg) to 500 lb (227.3 kg) (mean=216.4 lb [98.2 kg]). Fight times (including tag attachment) ranged from 4 to 85 minutes (mean=19.4 minutes). After tag placement, eight fish exhibited difficulty maintaining an upright orientation alongside the boat and were resuscitated for periods ranging from one to ten minutes before their release (Appendix 1).

All 61 PSATs reported after detachment from the fish. Two tags detached prematurely—both on the first day of deployment—and were excluded from survival analyses. The 59 tags that remained attached for the ten-day deployment period successfully transmitted between 18% and 96% (mean=81%) of the archived data. Most of these PSATs remained at sea during the data transmission period which typically lasts about 30 days before the battery power is exhausted. However, six tags washed ashore during the period of data transmission, resulting in reduced data reception from these tags. Two tags were recovered by beachcombers and returned to us, allowing recovery of 100% of the archived data.

We inferred the survival of 57 of 59 fish (96.6%) that carried the tags for the 10-day deployment from analyses of pressure (depth) and temperature profiles over the 10-day tagging period (Appendix 1). Surviving blue marlin exhibited multiple daily vertical movements as evidenced by the temperature and pressure (depth) profiles throughout the course of the ten-day tagging period. Many animals demonstrated a distinct diurnal patterning to their dives, remaining near the surface at night and making deep dives during the day (Fig. 2A). Net displacement ranged from 10 to 943 km (mean=226.9 km).

The two mortalities inferred from the PSAT data occurred among the 30 blue marlin caught on artificial lure and natural bait combinations rigged with J-hooks. Both individuals were hooked internally and bled profusely from the gill area at the time of capture. The archived data indicated that these individuals sank to the bottom shortly after release and remained there for 48–96 hr, after which time a release mechanism was activated by the constant depth data in each PSAT and initiated tag release and data transmission (Fig. 2B). The two mortalities of blue marlin caught on artificial lure and natural bait combinations with J hooks resulted in an estimated postrelease mortality rate of 6.7%. The results of 10,000 bootstrap simulations at an underlying true mortality of 6.7% indicated that the approximate 95% confidence intervals (CI) for the mortality estimates of blue marlin caught on J hooks for an experiment with 30 tags would range from 0% to 22% (with the methods of Goodyear, 2002). None of the 29 blue marlin caught on natural baits with circle hooks died during the ten day period, resulting in a postrelease mortality estimate of 0%, with corresponding 95% CI ranges from 0% to 12.5%. The difference between the estimates of postrelease mortality for blue marlin caught on J-hooks and circle hooks was not statistically significant (Fisher's exact test: P=0.26).

Discussion

The goal of this study was to determine whether blue marlin derive similar conservation benefits from the use of circle hooks in the recreational fishery as has been previously reported for other istiophorid billfishes. A direct comparison of hooking locations with the use of J hooks and circle hooks in natural baits rigged as they are typically fished in the recreational fishery indicates that the use of circle hooks results in sig-

nificantly lower rates of internal hooking locations for blue marlin, white marlin, and sailfish. We observed incidences of internal hooking locations with circle hooks ranging from 1.8% (blue marlin) to 6.2% (sailfish). The value of 2.0% (n=200) observed for white marlin is comparable to the value of 1.7% (n=59) reported for white marlin caught on natural baits with circle hooks (Graves and Horodysky, 2008). The incidence of internal hooking locations observed for circle hooks in sailfish (6.2%) is slightly higher than that reported by Prince et al. (2002) for Pacific sailfish caught on trolled natural baits with circle hooks (1.7%) but is within the range reported for circle hooks in live baits for both Atlantic sailfish (6–16%; Prince et al., 2007) and striped marlin (5–7%; Domeier et al., 2003).

The use of J hooks in natural baits resulted in incidences of internal hooking ranging from 19.1% (blue marlin) to 44.4% (white marlin). The frequency of internal hooking in white marlin caught with natural baits rigged with J hooks (44.4%) is similar to the value reported for white marlin caught on J hooks (50%) by Horodysky and Graves (2005). Internal hooking locations for sailfish caught on J hooks rigged with natural baits (41.2%) are comparable to results for Pacific sailfish caught on trolled dead baits rigged with J hooks (46.8%), and fall within the range reported for Atlantic sailfish caught on live baits rigged with J hooks using a variety of dropback times (23–57%; Prince et al., 2007), as well as striped marlin caught on live baits with J hooks (28%; Domeier et al., 2003). The use of J hooks resulted in a tenfold increase in internal hooking locations relative to circle hooks for blue marlin and a twentyfold increase for white marlin and sailfish—a trend also noted in previous studies of istiophorid billfish (Prince et al., 2002, 2007; Domeier et al., 2003; Horodysky and Graves, 2005).

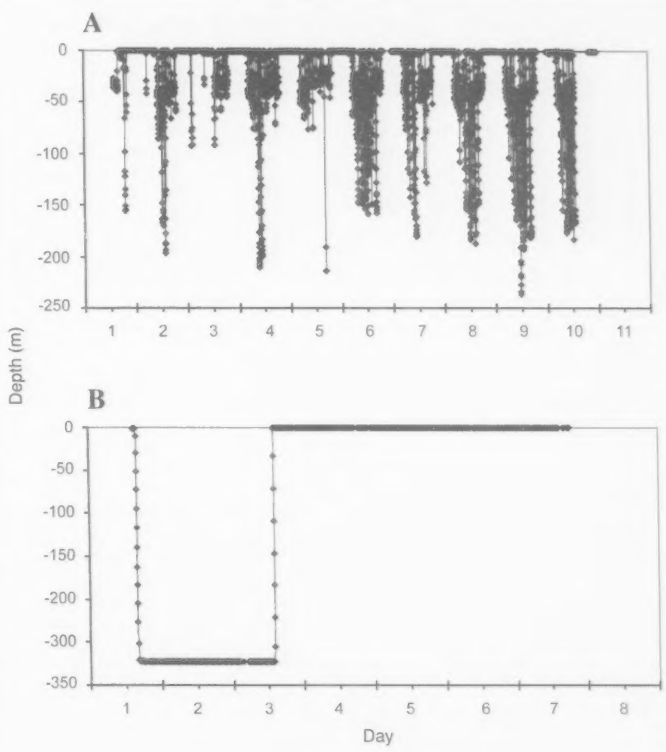

Figure 2

Depth plots derived from pop-up satellite archival tag pressure data for two blue marlin (*Makaira nigricans*) caught in the western Atlantic recreational fishery. (**A**) Blue marlin no. 49 was caught on a naked ballyhoo bait with a circle hook. This fish survived for the ten day tagging period and exhibited a strong diel pattern, diving during the day and remaining in surface waters at night. (**B**) Blue marlin no. 41 was caught on an artificial lure (Ilander) and ballyhoo combination bait with a J hook and was bleeding profusely from the gills at the time of capture. This fish died and sank to the bottom shortly after release. The release mechanism on the tag was activated by constant depth measurements for 48 hours and the tag floated to the surface and began transmitting data.

Although the frequency of internal hooking locations was significantly higher for blue marlin, white marlin, and sailfish caught on J hooks than on circle hooks, the rate of internal hooking locations for blue marlin caught on J hooks was less than half of the values observed for white marlin and sailfish. In a study of postrelease mortality in the recreational blue marlin fishery off Bermuda, Graves et al. (2002) reported no internal hooking locations for the nine blue marlin caught on artificial lures or artificial lure and natural bait combinations rigged with J hooks. The lower incidence of internal hooking locations for blue marlin caught on natural baits rigged with J hooks than for white marlin and sailfish caught on similar terminal tackle may result from interspecific differences in feeding ecology. Many billfishes follow trolled baits for a short time before striking, giving alert anglers an opportunity to pick up the rod and drop the bait back to the fish as it attacks. Dropback times of 5–10 s are common in the white marlin fishery (Mather et al., 1975; Jesien et al., 2006), and can be considerably longer in the sailfish live bait fisheries (Prince et al., 2007). By contrast, blue marlin are typically more aggressive feeders, often attacking the bait before anglers have an opportunity to react. When dropbacks are possible for this species, they are often of shorter duration than those for white marlin and sailfish, allowing less time for the bait to

be swallowed and hence for the hook to lodge in an undesirable location (Prince et al., 2007).

In previous studies, internal or deep hooking locations have been associated with an increased incidence of trauma in istiophorids and other large pelagic fishes (Domeier et al. 2003; Horodysky and Graves, 2005; Prince et al., 2007; Skomal, 2007). In the present study, trauma, as evidenced by bleeding, was significantly lower for blue marlin, white marlin, and sailfish caught on circle hooks than for those caught on J hooks. The low incidence of bleeding associated with natural baits rigged with circle hooks for white marlin that we observed (1.0%) concurs with the value of 1.7% reported for white marlin by Graves and Horodysky (2008) and the range reported for the congeneric striped marlin caught on live baits with circle hooks (3–4%, Domeier et al., 2003). The frequency of bleeding with circle hooks observed for sailfish (2.5%) in this study is slightly lower than the values reported for Pacific sailfish caught on natural baits (6%) and for Atlantic sailfish caught on live baits with circle hooks (5–13%; Prince et al., 2002, 2007). We noted bleeding in 33% of the white marlin and 33% of the sailfish caught on natural baits with J hooks. This value is somewhat lower than those reported for white marlin (45%) and Pacific sailfish (56.8%) caught on trolled natural baits, and higher than those reported for striped marlin (21%) and Atlantic sailfish (21–25%) caught on live baits (Prince et al., 2002, 2007; Domeier et al., 2003; Horodysky and Graves, 2005). The incidence of bleeding in white marlin and sailfish caught on J hooks was significantly higher than that for blue marlin caught on the same terminal tackle and is consistent with an increased incidence of internal hooking rates in the former species observed in this and previous studies (Prince et al., 2002; 2007; Domeier et al., 2003; Horodysky and Graves, 2005).

To directly follow the fate of blue marlin caught on trolled natural baits or on bait and lure combinations rigged with either circle or J hooks and released, we deployed 61 PSATs, of which 59 remained attached for the ten-day tracking period. All 29 blue marlin caught on circle hooks rigged with natural baits or bait and lure combinations survived for ten days after release. In a study of 59 white marlin caught on natural baits rigged with circle hooks, Graves and Horodysky (2008) reported a single mortality. Together, these studies reveal a very low level of postrelease mortality for billfishes caught on circle hooks in natural bait trolling fisheries. In contrast, Domeier et al. (2003) reported an adjusted rate of postrelease mortality of 17.4% for striped marlin caught from stationary vessels on live baits rigged with circle hooks. These results support the contention of Cooke and Suski (2004) that the magnitude of the conservation benefits of circle hooks varies among species, gear types, and fisheries.

PSAT depth records indicated that two of 30 blue marlin caught on artificial lure and natural combinations rigged with J hooks died after release, resulting in an estimated postrelease mortality of 6.7%. This value is approximately one-fifth of the postrelease mortality reported by Horodysky and Graves (2005) for 20 white marlin caught on natural baits rigged with J hooks (35%) and less than one-fourth of the value of 29.4% reported by Domeier et al. (2003) for 24 striped marlin caught on live baits rigged with J hooks. The reduction in postrelease mortality of blue marlin caught on natural baits with J hooks relative to postrelease mortality of white marlin caught on the same terminal tackle parallels the reductions observed in the frequency of internal hooking locations and bleeding between these species.

In this study, the use of circle hooks in natural baits resulted in significantly reduced internal hooking and bleeding for blue marlin, white marlin, and sailfish. Because blue marlin caught on J hooks experienced significantly lower incidences of internal hooking locations and trauma than white marlin and sailfish caught on the same terminal tackle, the conservation benefit resulting from the use of circle hooks for blue marlin is less than that experienced by the other two species. This asymmetry was also evident in the analysis of postrelease survival. There was a trend for decreased postrelease mortality of blue marlin caught on natural baits with circle hooks (0%) than for blue marlin caught on artificial lures and natural baits with J hooks (6.7%), but the difference was much smaller than that previously reported for white marlin caught on natural baits rigged with the two hook types (0% and 35%, respectively; Horodysky and Graves, 2005). Although these results provide support for recent management measures implemented by NMFS that require the use of non-offset circle hooks in natural baits for all Atlantic billfish tournaments, it is important to realize that the conservation benefits of this measure vary asymmetrically among the different billfish species.

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Appendix 1

Summary information for 61 blue marlin (*Makaira nigricans*) caught on different types of terminal tackle in the western Atlantic recreational fishery, tagged with pop-up satellite archival tags, and released. Fish were caught off Venezuela (VZ), the Dominican Republic (DR), Virginia (VA), North Carolina (NC), the U.S. Virgin Islands (VI), and Brazil (BR) on natural baits or combination baits consisting of an artificial lure (chugger [Chug], Ilander [I], or Sea Witch [Swi]), and natural bait rigged with J hooks (J) or circle hooks (C). Hook locations were recorded as internal (I) or external (E). Fight time included the tagging process and, where applicable, resuscitation ($R^{\text{duration in minutes}}$), and trauma (bleeding) at the time of release was noted as present (Y) or absent (N). Also included are the percentage of archived data recovered, mean straight line displacement (MSLD) over the 10-day tagging period, and fate of the blue marlin (coded as live [L], dead [D], or premature release [–]).

Fish	Date	Location	Gear (lb)	Established weight	Hook type	Hook location	Fight time	Trauma	Data (%)	MSLD (km)	Fate
1	9/7/07	VZ	30	200	Chug/J	I	55	N	82	172	L
2	3/17/08	VZ	50	175	I/J	E	28 R^{3}	N	81	139	L
3	3/28/08	DR	50	125	I/J	E	15 R^{2}	N	68	49	L
4	3/29/08	DR	50	100	C	E	30	N	85	86	L
5	5/15/08	VZ	30	165	C	E	18	N	84	30	L
6	5/15/08	VZ	30	100	Chug/C	E	5	N	85	10	L
7	5/16/08	VZ	50	160	I/J	E	5	Y	73	123	L
8	5/17/08	VZ	30	75	C	E	15	N	85	87	L
9	6/15/08	VA	50	400	I/J	E	56	N	85	546	L
10	6/22/08	NC	80	350	I/J	E	35	N	88	943	L
11	8/8/08	VI	50	450	I/J	E	18	N	90	502	L
12	8/10/8	VI	50	275	I/J	I	5	N	90	646	L
13	8/10/08	VI	50	350	Chug/C	E	8	N	92	349	L
14	8/11/08	VI	50	175	Chug/J	E	11	N	83	107	L
15	8/11/08	VI	50	175	Chug/C	E	4	N	88	343	L
16	8/12/08	VI	50	200	I/J	I	10	Y	93	488	L
17	8/12/08	VI	50	125	I/J	E	12	Y	87	328	L
18	8/17/08	NC	80	375	Swi/J	E	40	N	90	709	L
19	9/7/08	VI	50	160	I/J	E	20	N	91	191	L
20	9/7/08	VI	50	250	Chug/C	E	15	N	68	20	L
21	9/7/08	VI	50	235	C	E	22	N	92	319	L
22	9/8/08	VI	50	275	Chug/J	I	55	N	90	120	L
23	9/9/08	VI	50	125	I/J	I	14	N	93	238	L
24	9/10/08	VI	50	90	Chug/J	I	20 R^{10}	Y	72	68	L
25	9/10/08	VI	50	90	Chug/J	E	13	N	88	264	L
26	9/11/08	VI	80	325	I/J	E	35	N	100	197	L
27	9/15/08	VI	50	100	Chug/C	E	12	N	92	234	L
28	9/25/08	VZ	30	70	C	E	5	N	90	13	L
29	11/1/08	BR	130	300	Chug/C	E	11 R^{2}	N	85	119	L
30	11/2/08	VZ	30	150	Chug/C	E	21	N	84	336	L
31	11/3/08	VZ	30	290	C	E	85	N	94	171	L
32	11/4/08	BR	50	125	C	E	5	N	74	284	L
33	11/15/08	VZ	30	250	C	E	20	N	18	263	L
34	11/17/08	VZ	30	150	C	E	20	N	87	135	L
35	11/22/08	VZ	30	150	C	E	21	N	79	115	L
36	11/30/08	VZ	30	120	Chug/C	E	36 R^{4}	N	86	83	L
37	12/2/08	BR	130	200	Chug/J	I	12	Y	93	47	D
38	12/2/08	BR	130	175	Chug/C	E	5	N	36	289	L
39	12/9/08	VZ	30	125	Chug/C	I	21	N	81	226	L
40	12/9/08	VZ	50	100	I/J	E	6	N	90	118	L
41	12/9/08	VZ	50	200	I/J	I	9	Y	61	109	D

continued

Appendix 1 (continued)

Fish	Date	Location	Gear (lb)	Established weight	Hook type	Hook location	Fight time	Trauma	Data (%)	MSLD (km)	Fate
42	12/11/08	VZ	30	250	I/J	E	18	N	83	107	L
43	12/11/08	BR	130	450	Chug/C	E	10	N	85	218	L
44	12/12/08	BR	130	500	C	E	15	N	90	233	L
45	12/12/08	BR	50	400	C	E	12	N	91	216	L
46	1/2/09	BR	130	300	C	E	12	N	88	19	L
47	1/2/09	BR	130	400	Chug/C	E	10	N	94	329	L
48	2/7/09	VZ	80	145	Swi/J	E	10	N	26	124	L
49	4/18/09	VZ	80	115	C	E	14	N	85	96	L
50	5/6/09	VZ	50	265	I/J	E	34	N	57	88	L
51	5/9/09	VZ	50	110	C	E	10	N	100	90	L
52	7/6/09	VI	50	170	Chug/J	E	25 R[3]	N	85	70	—
53	7/6/9	VI	50	300	Chug/J	E	45 R[1]	N	80	196	L
54	7/9/09	VI	50	200	Chug/J	E	15	N	86	143	L
55	8/1/09	VI	50	250	Chug/C	E	15	N	38	109	L
56	8/8/09	VI	50	250	Chug/J	E	15	N	31	379	L
57	8/30/09	VI	50	175	C	E	20	N	93	80	—
58	9/2/09	VI	50	150	C	E	18	N	94	214	L
59	9/4/09	VI	50	350	C	E	16	N	96	463	L
60	9/30/09	VI	50	175	C	E	14	N	90	271	L
61	10/7/09	VI	50	200	I/J	E	40	N	92	385	L

Influence of ocean conditions on the timing of early life history events for blue rockfish (*Sebastes mystinus*) off California

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Abstract—Settled juvenile blue rockfish (*Sebastes mystinus*) were collected from two kelp beds approximately 335 km apart off Mendocino in northern California and Monterey in central California. A total of 112 rockfish were collected from both sites over 5 years (1993, 1994, 2001, 2002, and 2003). Total age, settlement date, age at settlement, and birth date were determined from otolith microstructure. Fish off Mendocino settled mostly in June and fish off Monterey settled mostly in May (average difference in settlement=23 days). Although the difference in the timing of settlement followed this same pattern for both areas over the five years, settlement occurred later in 2002 and 2003 than in the prior years of sampling. The difference in the timing of settlement was due primarily to differences in birth dates for the two areas. The time of settlement was positively related to upwelling and negatively related to sea level anomaly for most of the months before settlement. Knowledge of the timing of settlement has implications for design and placement of marine protected areas because protection of nursery grounds is frequently a major objective of these protected areas. The timing of settlement is also an important consideration in the planning of surveys of early recruits because mistimed surveys (caused by latitudinal differences in the timing of settlement) could produce biased estimates.

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Successful recruitment of fishes into adult populations can have a major influence on population biomass. Within a species, recruitment events can vary widely in magnitude both temporally and spatially (Doherty and Fowler, 1994; Ralston and Howard, 1995; Caley et al., 1996). Understanding this variability in recruitment strength is a critical goal in predicting adult population structure (Doherty and Fowler, 1994; Hidalgo et al., 2009). Knowledge of the spatial and temporal variability in recruitment of a population can lead to enhanced management of the species (e.g., to protection of important nursery areas) (Grorud-Colvert and Sponaugle, 2009).

Variation in recruitment strength is influenced by multiple biotic and abiotic factors, including the magnitude of spawning biomass, predation, available habitat, available prey, competition, temperature, upwelling, turbulence, water quality, and ocean currents (Peterman and Bradford, 1987; Ainley et al., 1993; Ralston and Howard, 1995; Hobson et al., 2001; Johnson et al., 2001; Sale et al., 2005; Hidalgo et al., 2009). Recruitment variability can occur from large-scale (e.g., El Niño or La Niña events, Pacific Decadal Oscillations) (Carr, 1991; Field and Ralston, 2005; Laidig et al., 2007) to small-scale processes (e.g., localized patchiness of suitable nursery habitats; fine-scale oceanographic events) (Sale et al., 2005; Johnson, 2006). Determining the relative influence of these processes on fish recruitment has been a goal for many studies (Peterman and Bradford, 1987; Yoklavich et al., 1996; Laidig et al., 2007).

Annual recruitment of rockfishes (*Sebastes* spp.) in the northeast Pacific can vary by orders of magnitudes between years (Ralston and Howard, 1995; Laidig et al., 2007). In addition to temporal variability in recruitment, latitudinal or spatial variability also has been observed for several rockfish species along the west coast (Sakuma et al., 2006). Variable recruitment leads to greater uncertainty in the prediction of year-class strength.

Rockfishes give birth to larvae (parturition) that survive in the plankton for several months before settling into nursery or adult habitats (Carr, 1991; Love et al., 2002; Ammann, 2004). For several rockfish species, it has been demonstrated that the strength of the year class is determined during this planktonic stage (Ralston and Howard, 1995; Laidig et al., 2007; Wilson et al., 2008) and that it can be affected further by postsettlement mortality from predation (Hobson et al., 2001).

In this study, the recruitment of juvenile blue rockfish (*S. mystinus*) from the pelagic environment to nearshore kelp beds was examined in two geographic regions along the California coast. Blue rockfish are an important commercial and recreational species in California ranging from at least British Columbia to northern Baja California (Love et al., 2002). Otolith microstructure was used to estimate

Table 1

Location, year, sampling date, number of samples collected, and size range of blue rockfish (*Sebastes mystinus*) examined for settlement marks in otoliths.

Location	Year	Sample date	Number of samples	Size range (mm standard length)
Mendocino	1993	2 Jun	11	37–48
Monterey	1993	3 Jun	11	38–48
Mendocino	1994	26 Jul	13	44–52
Monterey	1994	20 Jul	13	42–60
Mendocino	2001	11 Sep	10	48–70
Monterey	2001	5 Sep	10	53–68
Mendocino	2002	13 Aug	12	47–66
Monterey	2002	18 Jul	13	45–58
Mendocino	2003	4 Sep	10	58–73
Monterey	2003	1 Aug	9	47–59

the timing of settlement, birth dates, and length of the pelagic larval and juvenile stages of blue rockfish. Upwelling indices and sea level anomalies were used to evaluate the influence of oceanographic conditions on the timing of recruitment (settlement) for blue rockfish in the two regions.

Materials and methods

Juvenile blue rockfish were collected in two areas, approximately 335 km apart—one off northern California in Mendocino County (39°14′N lat., 123°46′W long.) and the other off central California along the southern edge of Monterey Bay in Monterey County (36°38′N lat., 121°55′W long.; Fig. 1). Each area is typified by large kelp beds that extend from shore to approximately 20 m depth. The Mendocino site is dominated by bull kelp (*Nereocystis luetkeana*) and the Monterey site by giant kelp (*Macrocystis pyrifera*). These kelp-bed areas comprise high-relief bedrock interspersed with low-relief cobble and sand areas. Both beds are exposed to open ocean conditions, although the Monterey site is slightly buffered from southerly seas by the tip of the Monterey Peninsula.

Fish were collected throughout the kelp beds by divers using small spears at depths of 5–20 m and were frozen for later analysis. Fish were collected during late spring and summer at both sites during five nonconsecutive years (1993, 1994, 2001–2003). Years for data analysis were selected on the basis of three criteria: 1) there were at least nine individuals collected from each area; 2) sampling dates at each study site in a particular year were reasonably close (approximately one month or less apart); and 3) samples were collected after 1 June to allow for complete settlement of the juveniles (Table 1).

Figure 1

Map of the two study areas along the California coast. Black stars indicate areas where samples of blue rockfish (*Sebastes mystinus*) were collected for otolith analysis to determine the timing of early life history events.

Otolith data

Sagittal otoliths were removed and ages were determined visually by counting growth increments with a compound microscope at 1000× magnification (Laidig et al., 1991), beginning at the first increment after the extrusion check (a mark in the otolith formed when the larvae were released from their mother). No validation of the rate of deposition of these growth increments was performed during this study, and none was available from the literature. However, based on validation studies for other co-occurring rockfish species, such as shortbelly rockfish (*S. jordani* [Laidig et al., 1991]), bocaccio (*S. paucispinis*), chilipepper (*S. goodei*), widow rockfish (*S. entomelas*), and yellowtail rockfish (*S. flavidus* [Woodbury and Ralston, 1991]), increments were assumed to be deposited daily. Also, the calculated birth dates of the blue rockfish in this study occurred within the months of larval release for this species (Wyllie-Echeverria, 1987).

The duration of the pelagic larval and juvenile stages, age at settlement (the total duration of pelagic larval and juvenile stages), settlement date, and birth date were calculated by identifying specific marks in the otolith that indicate transitions from one life stage to

the next. Transformation from the larval to the juvenile stage was ascertained by the occurrence of secondary growth primordia (areas of new increment growth that form away from the otolith core; Laidig et al., 1991). This transformation occurs during the planktonic stage before settlement. Duration of the pelagic juvenile stage was estimated as the number of increments occurring from the secondary growth primordia to the settlement mark. Settlement date was calculated by subtracting the number of increments formed after the settlement mark from the collection date, and birth date was determined by subtracting the total number of increments in the otolith from the collection date. The otolith increments deposited during the pelagic juvenile stage followed a regular pattern, increasing in width with fish age (Fig. 2). The settlement mark was the increment where a change in the depositional pattern of the increments was observed after the pelagic juvenile stage; typically the increment marking settlement is narrower than the preceding increments (Amdur, 1991). To be considered the settlement mark, this change in increment width had to be visible from the settlement mark to the outer edge of the otolith and not just in one section. Often the settlement mark was evident in the otolith as a dark ring of numerous closely spaced increments. After the settlement mark, increment widths followed no consistent growth pattern.

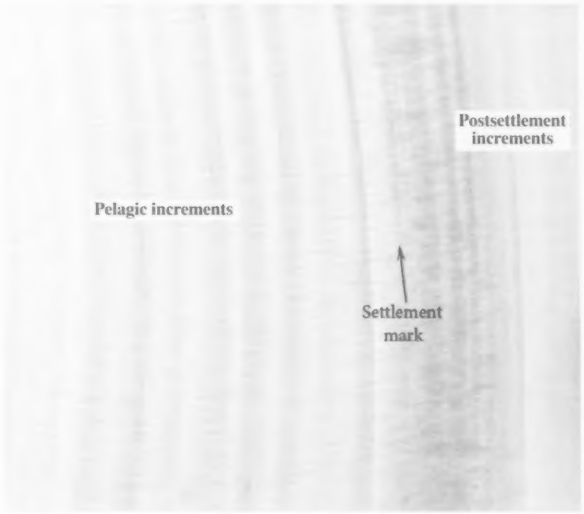

Figure 2

Growth increments in the otolith of a blue rockfish (*Sebastes mystinus*). The settlement mark and increments produced before (pelagic) and after (post) settlement are indicated.

Oceanographic data

Upwelling data were derived from monthly sea level pressure fields provided by the U.S. Navy Fleet Numerical Meteorology and Oceanography Center (data acquired from NMFS, Environmental Research Division, Southwest Fisheries Science Center at http://www.pfeg.noaa.gov, accessed July 2009) measured off Mendocino (39°11′N lat., 123°58′W long.) and Monterey (36°47′N lat., 122°24′W long.), California. Sea level anomaly data (adjusted for local atmospheric conditions) were collected from shore stations at Humboldt Bay (40°46′N lat., 124°13′W long.) and Monterey (36°36′N lat., 121°53′W long.), California, and monthly means were obtained from the University of Hawaii Sea Level Center. These data represent a measure of change in sea level height over time and reflect water movement a positive anomaly was associated with poleward flow and a negative anomaly was associated with equatorward flow.

Two-way analysis of variance was used to test the hypotheses that mean settlement date, mean birth date, mean duration of pelagic larval and juvenile stages, and mean settlement age did not differ significantly between the two study areas. Principal components analysis (PCA) was used to evaluate the relationship among the otolith data (settlement date, birth date, and settlement age) and the oceanographic variables (monthly average upwelling and sea level anomalies for January–June) for both areas. Canonical correlation analysis (CCA) of the oceanographic and otolith data was used to examine the possible causes of changes in interannual settlement dates.

Results

A total of 112 otoliths were examined (56 otoliths each from Mendocino and Monterey; Table 1). Sampling dates ranged from 2 June to 11 September each year, varying from 1 to 34 days between the two study areas in a particular year. Fish sizes ranged from 37 to 73 mm standard length (SL) for Mendocino and from 38 to 68 mm SL for Monterey.

Average birth dates varied annually, with a difference of 7–30 days between locations and an average of 19 days difference over all years (Fig. 3). Birth dates of Mendocino rockfish were always later in the year than those of rockfish from Monterey (significantly different in 1994, 2001, and 2002; $P<0.05$). Birth dates ranged from 4 January to 25 March for Mendocino fish (7 February average) and from 22 December to 9 March for Monterey fish (19 January average).

Average settlement dates were significantly different ($P<0.001$) each year between the two locations, with fish from Mendocino always settling later in the year than fish from Monterey (23 days average; Fig. 4). The difference in settlement between the two sites varied from an average of 17 to 29 days. The earliest date of

settlement was 17 May 1993 for fish off Mendocino and 23 April (occurring in both 2001 and 1993) for fish from Monterey; the latest settlement date was 1 July 2002 for fish off Mendocino and 4 June 2002 for fish off Monterey. Settlement dates were later in 2002 and 2003 and earlier in 1993 than in the other years.

The duration of the larval and pelagic juvenile stages was not significantly different between the two areas in any particular year (Figs. 5 and 6). The average duration for the larval stage was 69 days (range=41–100 d) for fish off Mendocino and 68 days (range=47–90 d) for fish off Monterey. The average duration for the pelagic juvenile stage was 56 days (range=26–90 d) for fish off Mendocino and 52 days (range=14–81 d) for fish off Monterey. Duration of pelagic larval and juvenile stages generally was longer for fish born in the 2000s than for fish born in the 1990s. Fish settled at younger ages at both study sites in the 1990s than in the 2000s (Fig. 7). Age at settlement was significantly different ($P<0.05$) between the two locations only in 2003; fish from Mendocino settled at an older age than those from Monterey.

From the PCA, 56% of the variability in otolith data was explained by the first eigenvector for fish off Mendocino and Monterey. This vector was characterized by the inverse relationship of birth date and settlement age, i.e., the earlier the birth date, the older the settlement age. The second eigenvector explained 41% and 39% of the variability in otolith data for fish off Mendocino and Monterey, respectively; this vector was characterized by later settlement dates and birth dates. The first eigenvector for oceanographic data explained 60% of the variability from Mendocino and 61% of the variability in data from Monterey; this vector was associated with the inverse relationship of upwelling and sea level during the months of March through June off Mendocino and May and June off Monterey. The second eigenvector in the oceanographic data was related to the inverse relationship between upwelling and sea level in April at both sites and explained 30% and 28% of the variability in data from Mendocino and Monterey, respectively.

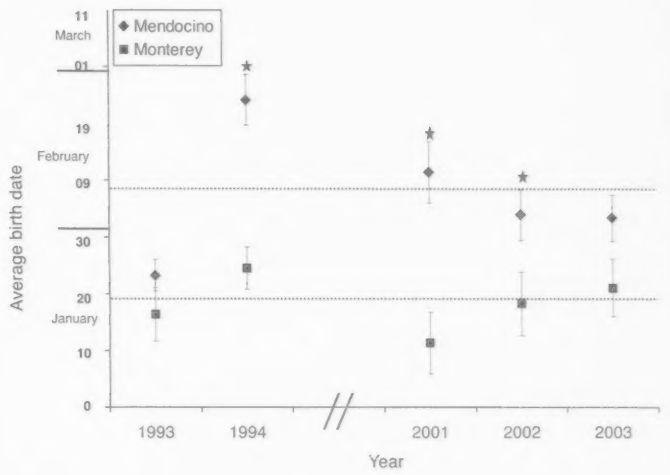

Figure 3

Average birth dates (in calendar days), back-calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas in California. Black stars indicate significant differences ($P<0.05$) between study areas for a particular year. Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error. Horizontal lines on the *y* axis separate months.

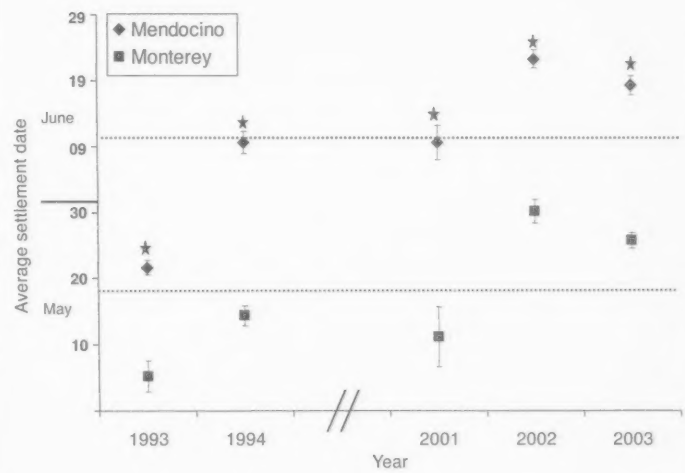

Figure 4

Average settlement dates (in calendar days), back-calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas in California. Black stars indicate significant differences ($P<0.001$). Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error. Horizontal lines on the *y* axis separate months.

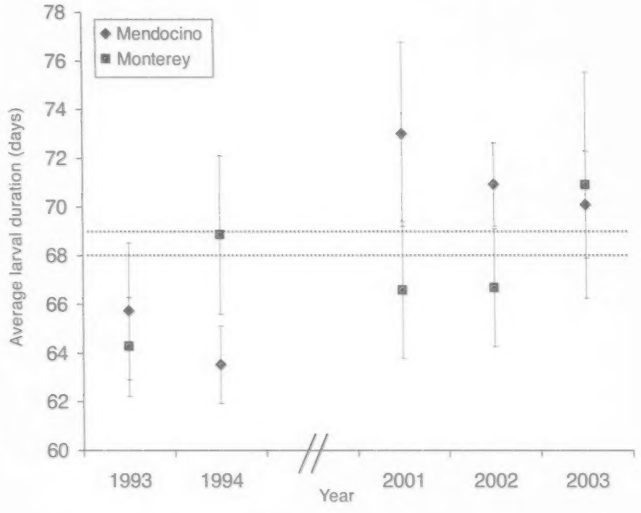

Figure 5

Average larval duration, calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas off California. Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error.

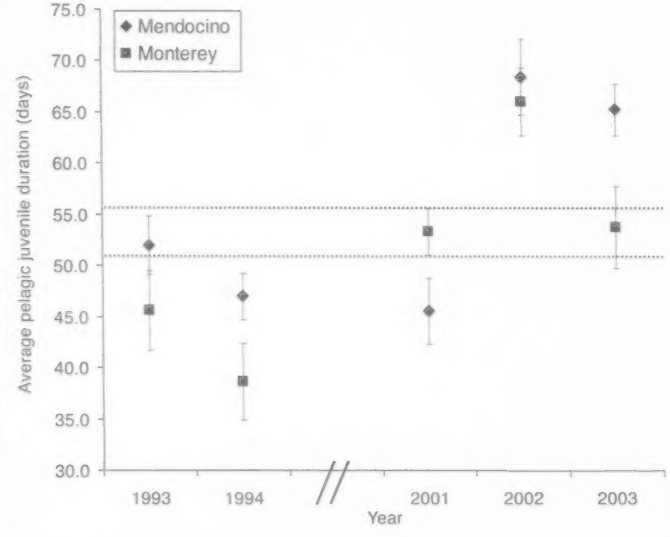

Figure 6

Average pelagic juvenile duration, calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas off California. Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error.

Results from the CCA were similar for data from both study areas (Fig. 8). For Mendocino, settlement dates later in the year (later than the average date for a particular year) were positively related to upwelling in February, May, and June, and inversely related to sea level anomalies in February, March, and May. For Monterey, later settlement dates were positively related to upwelling in all months, except April, and negatively related to sea level anomalies in all months, except April. There was an inverse relationship between birth date and settlement age for both sites, whereby an early birth date corresponded with an older settlement age.

Discussion

The timing of settlement of blue rockfish was related primarily to the timing of birth. Blue rockfish off Mendocino that settled on average three weeks later than fish off Monterey also were born, on average, about three weeks later than fish off Monterey. The age at settlement did not differ significantly between sites, nor did the duration of the larval or pelagic juvenile stages. Pasten et al. (2003) also attributed differences in settling date to time of parturition because early settlers of *Sebastes inermis* to seagrass beds in Japan were born earlier than late-settling fish. These researchers concluded that there was an ideal size for settlement and for active migration. Sogard et al. (2008) studied the maternal effects of rockfishes on their progeny and postulated that factors influencing the time of parturition also influenced recruitment success. It must be noted that parturition dates for blue rockfish in the present study were calculated from surviving juveniles. Those juveniles that did not survive may have been born at a different time and therefore would change the average parturition date (Woodbury and Ralston, 1991; Yoklavich et al., 1996). However, because no estimate of early larval or juvenile mortality exists for blue rockfish, I could not adjust for this effect.

Time of spawning and parturition of many fish species vary by latitude. Parturition dates for numerous eastern Pacific rockfish species occur later in northern study areas off Washington and Alaska than in areas off California

(Wyllie-Echeverria, 1987). Plaza et al. (2004) determined that parturition of *S. inermis* occurred later in the season at the more northerly sites in the western Pacific and suggested that this difference may be related to environmental cues. Vinagre et al. (2008a, 2008b) reported a latitudinal gradient in time of spawning for European sea bass (*Dicentrarchus labrax*) and common sole (*Solea solea*) off Portugal and that spawning onset occurs earlier in the south. These researchers suggested that warm water temperatures in winter at lower latitudes or differences in photoperiod may influence the onset of spawning.

The latitudinal difference in the timing of settlement and parturition in blue rockfish could be an adaptation by blue rockfish to oceanic conditions. Bograd et al. (2009) calculated the spring transition index (i.e., the beginning of the upwelling season) and found that upwelling began on average 20 days earlier off Monterey than off Mendocino. This difference is similar to the 23-day average difference in settlement timing between these two areas. It is possible that blue rockfish have adapted to this difference in the timing of upwelling.

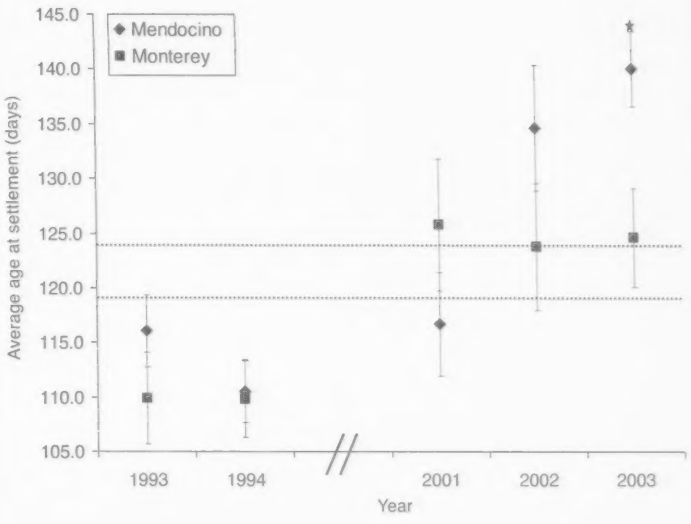

Figure 7

Average age at settlement, calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas off California. Black stars indicate significant differences ($P<0.05$). Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error.

Interannual variability in parturition dates has been noted by researchers, but specific causes for this variability are still unknown. Woodbury and Ralston (1991) observed variations in the timing of parturition for five species of rockfishes over six years. Early parturition dates have been related to increased maternal age and size for some rockfish species (Bobko and Berkeley, 2004; Plaza et al., 2004; Sogard et al., 2008). Plaza et al. (2004) proposed that the time of parturition could be influenced by effects of temperature on gestation times. Carr (1991) suggested that upwelling may influence the time of parturition. Interestingly, positive upwelling in January and February in this study was correlated with settlement date and this finding strengthens Carr's speculation.

Interannual variability in settlement date was related to upwelling and sea level height in this study. Settlement occurred later in years when upwelling was stronger and sea level anomaly was negative (i.e., there was an equatorward flow of cold water). Stronger upwelling may have transported juvenile rockfish farther offshore, making their return to the nearshore more difficult and causing successful recruitment to occur later in the season (Ainley et al., 1993; Larson et al., 1994; Sakuma et al., 2006; Wilson et al., 2008). Years with reduced or negative upwelling should result in onshore transport and thus earlier settlement to nearshore areas. Cold water produced by upwelling or flow from the north may result in slow growth of juvenile rockfishes (Boehlert and Yoklavich, 1983). These slow-growing individuals may migrate slowly to the nearshore environment. If prey are plentiful, the fish may remain in these food-rich waters longer or, if the quality of the prey items was low, the fish may exhibit reduced growth rates (Boldt and Rooper, 2009). Both of these factors could lead to later settlement of individuals.

Large-scale oceanographic processes (covering 100s of kilometers) can be important in determining recruitment strength over a broad area. Field and Ralston (2005) concluded that the synchrony in year-to-year recruitment for three rockfish species along the west coast of North America was caused by large-scale ocean processes (i.e., El Niño and Pacific Decadal Oscillation). Ralston and Howard (1995) reported similar recruitment strengths in blue and yellowtail rockfishes from two areas off California over a 10-year period and suggested large-scale ocean processes that affect sea surface temperatures (such as El Niño) are primarily responsible for the recruitment variation. Laidig et al. (2003) estimated similar ages and growth curves for adult blue rockfish from Mendocino and Monterey, which indicated that the fish from these areas are influenced by similar oceanographic conditions.

Understanding the causal relationship of biologic and oceanographic factors on recruitment dynam-

ics has implications for fisheries management. For instance, the design and placement of marine protected areas can be augmented to include areas where juvenile rockfishes are recruited and grow, increasing the likelihood of sustained production for those rockfish species. Recruitment dynamics also need to be considered when conducting surveys of rockfish populations early in their life. These surveys can lead to enhanced recruitment predictions for the fishery. However, without information on the spatial and temporal occurrence of recruitment, surveys could be mistimed in a particular region and lead to biased estimates. Results of the present study indicate that coastwide recruitment surveys should be conducted from south to north to allow for later spawning times with increased latitude.

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The work of all the divers who helped over the five years, especially T. Chess, T. Hobson, D. Howard, D. VenTresca, A. Ammann, and K. Baltz is greatly appreciated. M. Yoklavich and D. Watters offered helpful suggestions during this study. I also thank A. Ammann, S. Lonhart, K. Sakuma, B. Wells, M. Yoklavich, and three anonymous reviewers for their helpful comments of this manuscript.

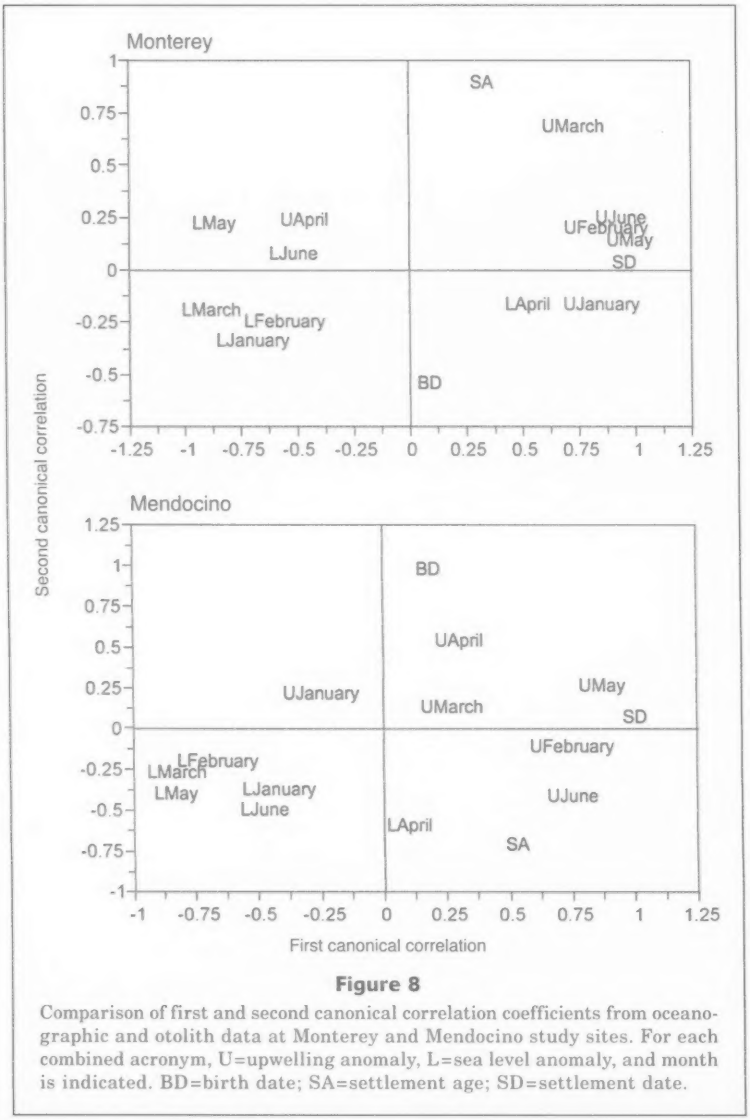

Figure 8

Comparison of first and second canonical correlation coefficients from oceanographic and otolith data at Monterey and Mendocino study sites. For each combined acronym, U=upwelling anomaly, L=sea level anomaly, and month is indicated. BD=birth date; SA=settlement age; SD=settlement date.

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Abundance and distribution of Atlantic sturgeon (*Acipenser oxyrinchus*) within the Northwest Atlantic Ocean, determined from five fishery-independent surveys

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Abstract—A lack of knowledge of how oceanic habitat is used by juvenile marine migrant Atlantic sturgeon (*Acipenser oxyrinchus*) is hindering conservation measures directed at restoring severely depleted populations. Identifying the spatial distribution of Atlantic sturgeon is necessary to identify critical habitat and appropriate management actions. We used five fishery-independent surveys to assess habitat use and movement of Atlantic sturgeon during their marine life stage. The size distribution ranged from 56 to 269 cm total length (mean=108 cm). Ninety-eight percent of all Atlantic sturgeon were smaller than 197 cm—a size that indicated the majority were immature. The pattern of habitat use revealed concentration areas and potential migration pathways used for northerly summer and southerly winter migrations. Atlantic sturgeon were largely confined to water depths less than 20 m and aggregations tended to occur at the mouths of large bays (Chesapeake and Delaware bays) or estuaries (Hudson and Kennebec rivers) during the fall and spring and to disperse throughout the Mid-Atlantic Bight during the winter. In most surveys depth, temperature, and salinity were significantly related to the distribution of Atlantic sturgeon. Knowledge of their habitat and movements can be used to devise spatially based conservation plans to minimize bycatch and to enhance population recovery.

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The Atlantic sturgeon (*Acipenser oxyrinchus*) is a long-lived anadromous fish with a historic range from Hamilton Inlet on the coast of Labrador to the Saint Johns River in Florida (Smith and Clugston, 1997). A major commercial fishery once existed throughout the historic range and estimated U.S. landings peaked at 3.3 million kg in 1890 (Smith and Clugston, 1997). Unable to support such intensive fishing, Atlantic sturgeon populations collapsed throughout the eastern seaboard by 1901 (Secor et al., 2002). During the late 1900s, there was a brief re-emergence of the Atlantic sturgeon fishery in New York and New Jersey (Kahnle et al., 2007) and landings peaked at 125,000 kg in the late 1980s (Waldman et al., 1996; Bain et al., 2000). In 1990 the Atlantic States Marine Fisheries Commission (ASMFC) developed a fishery management plan for the conservation and restoration of Atlantic sturgeon in order to restore population levels that would support harvests at 10% of the historical peak landings (ASMFC[1]). With a continued decline in the population, a 1998 ASMFC amendment began a 40-year moratorium in order to protect 20 year classes of spawning females (ASMFC[2]). Currently, Atlantic sturgeon are a candidate species to be listed under the United States Endangered Species Act.

Atlantic sturgeon use river, estuarine, coastal, and oceanic environments at different life stages but spend the majority of their lives in saltwater (Smith and Clugston, 1997). However, information on oceanic habitat use is lacking beyond evidence of broad-scale marine migrations and an exchange of populations among river systems based on tag recaptures (Dovel and Berggren, 1983) and commercial fisheries bycatch data (Stein et al., 2004a, 2004b). Fisheries-dependent data indicate that most At-

[1] Atlantic States Marine Fisheries Commission (ASMFC). 1990. Fishery management plan for Atlantic sturgeon. Fishery management report number 17, 85 p. ASMFC, Washington, D.C.

[2] Atlantic States Marine Fisheries Commission (ASMFC). 1998. Amendment 1 to the interstate fishery management plan for Atlantic sturgeon, Fishery Management report 31, 59 p. ASMFC, Washington, D.C.

lantic sturgeon inhabit shallow inshore areas of the continental shelf (Stein et al., 2004a, 2004b). More recently, some long-term fishery-independent data have revealed that juvenile Atlantic sturgeon use the inshore waters of North Carolina during the winter months (Laney et al., 2007). Additionally, there are a handful of reported cases of Atlantic sturgeon captured in deeper offshore areas (Timoshkin, 1968; Collins and Smith, 1997; Stein et al., 2004a, 2004b). Still, more information is needed to guide management towards the best mechanisms to protect the remaining Atlantic sturgeon.

One contributing factor to the continued decline of Atlantic sturgeon populations is incidental capture of juveniles in non-target marine fisheries (Collins et al., 1996; Stein et al., 2004a). Most of the current bycatch mortality occurs in gill and drift net fisheries (Stein et al., 2004a; ASSRT[3]). Discard mortality from trawl fisheries is hard to estimate because few direct mortalities are observed. Mortality however may be very high due to delayed effects on captured individuals (Davis, 2002; Broadhurst et al., 2006). Because Atlantic sturgeon do not reach maturity until 12–14 years of age and reproductive output increases later in life (Van Eenennaam and Doroshov, 1998), reducing mortality on juveniles is key to restoring depleted populations (Boreman, 1997).

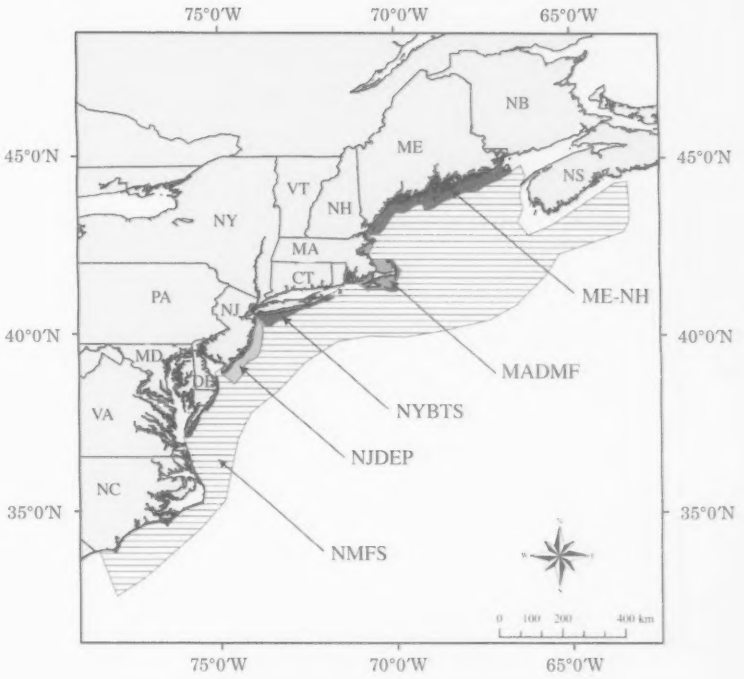

Figure 1

Coverage area of the Maine-New Hampshire inshore bottom trawl survey (ME-NH), Massachusetts Division of Marine Fisheries bottom trawl survey (MADMF), New York bottom trawl survey (NYBTS), New Jersey Department of Environmental Protection finfish survey (NJDEP), and the National Marine Fisheries Service bottom trawl surveys (NMFS). The area covered by the NMFS survey is represented by horizontal stripes. All other surveys are represented by shades of gray.

In order to adequately protect both juvenile and adult Atlantic sturgeon, marine distributional patterns must be identified such that essential habitat may be protected. In this article we use data from five different oceanic fishery-independent surveys to reveal the seasonal distribution, abundance, and habitat use of Atlantic sturgeon along the Northwest Atlantic continental shelf from Cape Hatteras, NC, to the Gulf of Maine (GOM) (Fig. 1).

Materials and methods

We analyzed data from five fishery-independent surveys conducted by the following agencies: 1) National Marine Fisheries Service (NMFS); 2) New Jersey Department of Environmental Protection (NJDEP); 3) Maine Department of Marine Resources and the New Hampshire Fish and Game Department (ME-NH); 4), Massachusetts Division of Marine Fisheries (MADMF); and 5) New York Bottom Trawl Survey (NYBTS) (Fig. 1). Catch per unit of effort (CPUE) was calculated (number of fish per tow) for each survey and depth (m). Depth (m), temperature (°C), and salinity (ppt) data were obtained from the NMFS, NJDEP, and NYBTS databases to estimate environmental preferences. For all surveys, except the MADMF, depth was calculated as the average between the maximum and minimum values. Depth values used in the MADMF analysis are the depth at which the tow started. For all surveys, tows were analyzed for each season, which are defined as winter (21 Dec–20 Mar), spring (21 Mar–20 Jun), summer (21 Jun–20 Sept), and fall (21 Sep–20 Dec). Specifics of each survey are discussed in detail below.

Because male and female Atlantic sturgeon mature at different size ranges (van Eenennaam and Doroshov,

[3] Atlantic Sturgeon Status Review Team (ASSRT). 2007. Status review of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*), 174 p. Report to National Marine Fisheries Service, Northeast Regional Office, Gloucester, MA, 23 Feb 2007. National Oceanic and Atmospheric Science Administration, Washington D.C.

1998) and because we could not distinguish between gender, we applied female size at maturation to all individuals. Female maturation is reached at a total length of 197 cm (van Eenennaam and Doroshov, 1998).

NMFS bottom trawl survey

These surveys were conducted primarily by the research vessels *Albatross IV* and *Delaware II* where a Yankee 36 bottom trawl with a 1.27-cm mesh liner was towed for 30 minutes at 3.79 knots. Sampling was conducted during the day and night (Sosebee and Cadrin[4]). A total of 300–400 trawls were executed each season from the Gulf of Maine to just south of Cape Hatteras, NC (Fig. 1). Sampling for the NMFS fall survey began in 1963 and the waters of southern New England and the Gulf of Maine were sampled before tows were expanded to include inshore stations in 1973. The NMFS survey was further expanded to include spring samples in 1973. We also used some additional NMFS surveys that were conducted during the winters of 1964–66, 1972, 1978, 1981, and 1992–2007, and summers of 1977–81 and 1993–95.

NJDEP finfish survey

The NJDEP finfish survey began in 1988 and is conducted five times per year in April, June, August, October, and January. A total of 186 tows are conducted each year (39 stations per trip for spring–fall months and 30 stations per trip for winter months). Sampling occurred from NY Harbor to the entrance of Delaware Bay, DE, from 8 to 30 m depth (Fig. 1). A depth-stratified random sampling design was used and a minimum of 10 tows were completed per depth interval (0–10 m, 10–20 m, and 20–30 m). The survey was conducted with a three-to-one two-seam trawl (25-m headrope, 30.5-m footrope) with 12-cm stretched mesh forward netting that tapered down to 8-cm stretched mesh rear netting that was lined with a 6.4-mm mesh codend liner. Tows were conducted at a speed of 3–3.5 knots for a duration of 20 minutes during daylight hours.

ME-NH inshore bottom trawl survey

This survey began in fall of 2000 and primarily covered the inshore waters of Maine and New Hampshire and a depth range of 9–150 m and distance up to 19.3 km offshore (in accordance with the 12-mile territorial limit) (Fig. 1). A total of 115 trawls were attempted each fall and spring. 100 stations were selected on the basis of a depth-stratified, random sampling design and of the 100 stations, 15 were fixed location stations. For this survey a 57–70 modified shrimp trawl (17.37-m head rope, 21.34-m footrope) was used with 5.08-cm stretched mesh and a 2.54-cm stretched mesh liner in the codend. Tows were conducted for 20 minutes at 2.2–2.3 knots during daylight hours.

MADMF bottom trawl survey

Conducted during the spring and fall from 1978–2007, this bottom trawl survey encompassed the Massachusetts inshore waters up to 5.6 km from the boundaries of New Hampshire and Rhode Island (Fig. 1). A ¾ size North Atlantic two-seam otter trawl (head rope 11.9 m, footrope 15.5 m) with a 6.4-mm lined codend was towed at 2.5 knots for 20 min during daylight hours. The survey sampled 100 stations per year selected using a depth-stratified, random sampling design.

New York bottom trawl surveys (NYBTS)

The NY surveys consisted of two surveys—the New York young-of-the-year bluefish survey and the NY trawl survey for subadult Atlantic sturgeon. The sampling area encompassed the waters inshore of a depth of 30 m; the practical inshore limit was 8–10 m from Montauk Point to the entrance of NY Harbor (Fig. 1). For this survey a depth-stratified sampling design was used with strata based on the depth intervals 0–10 m, 10–20 m, and 20–30 m. Tows were randomly selected by using a random number generator and were conducted for a duration of 20 minutes at a tow speed of 3–3.5 knots during daylight hours. The net was a three-to-one two-seam trawl (25-m headrope, 30.6-m footrope) with forward netting of 12-cm stretched mesh tapering down to the rear netting of 8-cm stretched mesh and lined with a 6.0-mm mesh liner within the codend. Because exactly the same gear was used for the surveys, they were combined for the purpose of this analysis. Further differences between the two surveys are described below.

The NY young-of-the-year bluefish survey was initially restricted to the 10- and 20-m depth strata where 10 tows per depth stratum were completed for a total of 20 tows per cruise. Sampling took place June–October in 2005 and August–September in 2006. The survey was confined to the 10-m depth strata in September, October, and November of 2007 when 25, 24, and 27 tows were completed, respectively.

For the NY trawl survey for subadult Atlantic sturgeon, a total of 10 cruises were conducted from October 2005 through June 2007 with 30 tows per cruise distributed within the 10-, 20-, and 30-m depth strata. Sampling months were October, November, January, April, May, and June. A total of 10 tows were completed for each depth. In June 2007, 36 tows were confined to the 10-m depth stratum.

Spatial analysis

Atlantic sturgeon captures were mapped by season with ESRI® ArcGIS™, vers. 9.2 software (ESRI; Redlands,

[4] Sosebee, K. A., and S. X. Cadrin. 2006. A historical perspective on the abundance and biomass of northeast demersal complex stocks from NMFS and Massachusetts inshore bottom trawl surveys, 1963–2002. NEFSC Ref. Doc. 06-05, 200 p. Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole Laboratory, 166 Water St., Woods Hole, MA 02543.

CA). Map base layers were obtained from the United States Geological Survey Coastal and Marine Geology Program GIS catalogue. Atlantic sturgeon captures were plotted by using graduated symbols in the following categories: 1, 2, 3–4, 5–10, 11–14, and >15 Atlantic sturgeon per tow.

Habitat preferences

We estimated the habitat preference of Atlantic sturgeon by using the catch-weighted methods of Perry and Smith (1994) for correcting bias that arises in stratified surveys where sampling effort differs between strata. With this method, a comparison of a catch-weighted cumulative distribution of available (all habitat sampled) and occupied (habitat where Atlantic sturgeon were captured) habitat was made and a randomization routine was used to estimate whether the occupied habitat was significantly different from available habitat. Habitat variables analyzed included temperature, dissolved oxygen, and salinity.

The cumulative distribution function (cdf) of the environmental variable was calculated with the following function:

$$f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{hi}), \quad (1)$$

where W_h = the proportion of the survey in stratum h;
n_h = the number of tows in stratum h;
x_{hi} = the habitat variable in tow i and stratum h; and
I = an indicator function where

$$I(x_{hi}) = \begin{cases} 1, & \text{if } x_{hi} \le t \\ 0, & \text{otherwise} \end{cases}. \quad (2)$$

The following function relates the catch weighted cdf to the habitat variable:

$$g(t) = \sum \sum \frac{W_h}{n_h} \frac{y_{hi}}{\bar{y}_{st}} I(x_{hi}), \quad (3)$$

where y_{hi} = the number of fish captured in tow i in stratum h; and
y_{st} = the stratified mean abundance.

The strength of the association is measured by the difference between the available and occupied cdf:

$$\max\left|g(t) - f(t)\right| = \max\left|\sum_h \sum_i \frac{W_h}{n_h}\left(\frac{y_{hi} - \bar{y}_{st}}{\bar{y}_{st}}\right)(x_{hi})\right|. \quad (4)$$

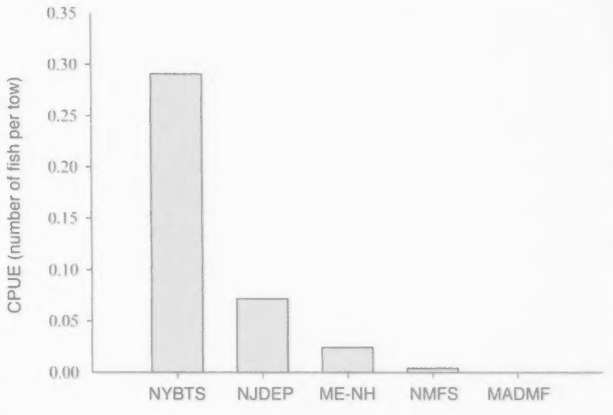

Figure 2

Catch per unit of effort (CPUE) for Atlantic sturgeon (*Acipenser oxyrinchus*) during the New York bottom trawl survey (NYBTS), New Jersey Department of Environmental Protection finfish survey (NJDEP), Maine-New Hampshire inshore bottom trawl survey (ME-NH), National Marine Fisheries Service bottom trawl surveys (NMFS), and Massachusetts Division of Marine Fisheries bottom trawl survey (MADMF).

Significance is determined by randomizing for 1000 trials the pairings of x_{hi} and (W_h/n_h) $(y_{hi} - \bar{y}_{st})/\bar{y}_{st}$ and by dividing the number of trials that are greater than the test statistic by the total number of trials.

Results

The NYBTS had the highest CPUE (0.291 fish/tow), followed by the NJDEP finfish survey (0.072 fish/tow), ME-NH inshore bottom trawl survey (0.024 fish/tow), NMFS bottom trawl survey (0.004 fish/tow), and the MADMF bottom trawl survey (<0.001fish/tow), in the latter of which only one Atlantic sturgeon has ever been captured (Table 1; Fig. 2). The details of the CPUE by depth (Fig. 3) and seasonal distribution and abundance (Fig. 4–7) for each survey are reported in detail below. Total length of Atlantic sturgeon captured within the surveys ranged from 56 to 269 cm (mean=108 cm) (Table 2; Fig. 8).

NMFS bottom trawl survey

A total of 107 Atlantic sturgeon were captured in 27,420 bottom trawls (Table 1). The depth distribution of completed tows ranged from 5 to 542 m deep, and 5214 peak tows occurred between 20 and 40 m (Fig. 3A). CPUE of Atlantic sturgeon was highest for the 10-m depth stratum (0.0273/tow) and decreased with each depth interval (Fig. 3A). A total of 71.30% of the Atlantic sturgeon were captured in 20 m or less and no individuals were captured in water deeper than 30 m (Fig. 3A). Atlantic

Table 1

Summary of the surveys effort and Atlantic sturgeon (*Acipenser oxyrinchus*) captures for the New York bottom trawl survey (NYBTS), New Jersey Department of Environmental Protection (NJDEP) finfish survey, National Marine Fisheries Service (NMFS) bottom trawl survey, Maine Department of Marine Resources and New Hampshire Fish and Game (ME-NH) inshore trawl survey, and Massachusetts Division of Marine Fisheries (MADMF) bottom trawl survey. Seasons are defined as winter (21 Dec–20 Mar), spring (21 Mar–20 Jun), summer (21 Jun–20 Sep), and fall (21 Sep–20 Dec).

Survey	Time period	Total number of trawls completed	Total number of Atlantic sturgeon captured	Catch per unit of effort
NYBTS	2005–07	512	149	0.291
	fall	132	46	0.348
	winter	59	4	0.068
	spring	219	73	0.333
	summer	102	26	0.255
NJDEP	1988–2007	3617	261	0.072
	fall	769	74	0.096
	winter	599	74	0.124
	spring	1439	113	0.079
	summer	810	0	0.000
NMFS	1973–2007	27,420	107	0.004
	fall	11,919	26	0.002
	winter	2563	12	0.005
	spring	11,395	68	0.006
	summer	1543	1	0.001
ME-NH	2000–06	1601	38	0.024
	fall	773	31	0.040
	spring	828	7	0.008
MADMF	1978–2007	5563	1	>0.001
	spring	2874	1	>0.001
	fall	2689	0	>0.001

Table 2

Mean, standard deviation, and range of total length (cm) of Atlantic sturgeon (*Acipenser oxyrinchus*) captured in the New York bottom trawl survey (NYBTS), New Jersey Department of Environmental Protection (NJDEP) finfish survey, National Marine Fisheries Service (NMFS) bottom trawl survey, Maine Department of Marine Resources and New Hampshire Fish and Game (ME-NH) inshore trawl survey, and Massachusetts Division of Marine Fisheries (MADMF) bottom trawl survey. Length information includes all recorded lengths over the duration of the entire period of the above surveys.

Survey	Mean total length ±standard deviation (cm)	Range (cm)
NYBTS	112.01 ±27.75	72–215
NJDEP	103.89 ±32.13	52–248
NMFS	113.87 ±40.18	51–269
ME-NH	115.4 ±19.39	76–152
MADMF	78 ±0	—

sturgeon were captured during all seasons but were most abundant during the spring, with an average CPUE of 0.006 fish/tow, followed by winter (0.005 fish/tow), fall (0.002 fish/tow), and summer (0.001 fish/tow) (Table 1).

In the spring, 70.59% of Atlantic sturgeon were captured in Virginia (VA) and NC waters and 23.53% were captured in NY and NJ. One Atlantic sturgeon was captured south of Cape Hatteras and one was captured offshore of northern MA. During winter months captures were evenly distributed from NJ to NC. A total of 42.30% (11 fish) of fall captures occurred off Long Island, NY, whereas 30.76% (8 fish) occurred in the mouth of Delaware Bay, Delaware (DE). In addition three fish were captured in NJ, one fish south of Cape Hatteras, and one fish near Cape Cod, MA. Only one Atlantic sturgeon was captured during this survey in the summer months in NY waters off of Long Island.

NJDEP finfish survey

A total of 261 Atlantic sturgeon were captured within 3617 bottom trawls from 1988 through 2007 (Table 1) at all depths sampled (Fig. 3B). Tow distribution ranged

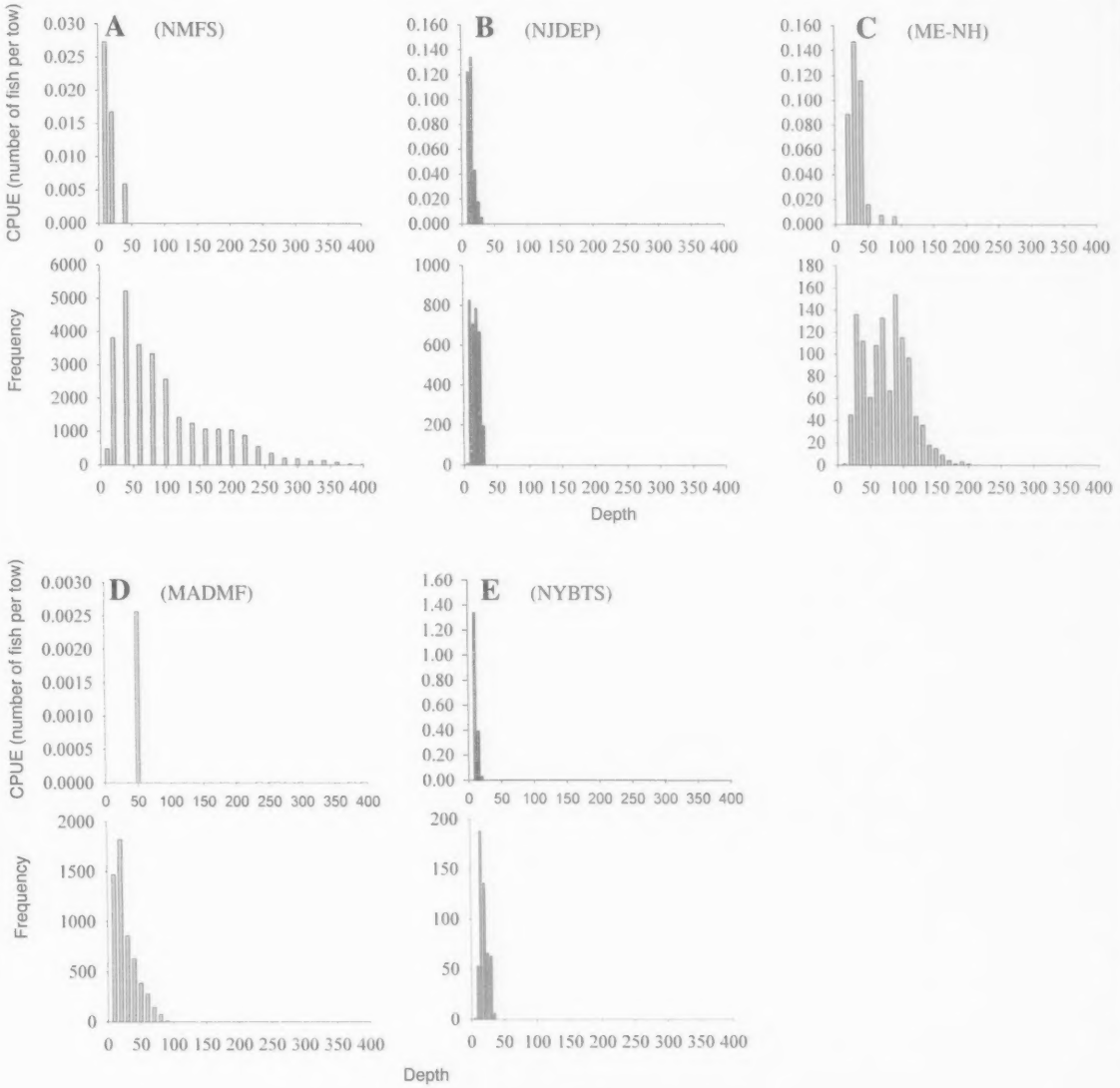

Figure 3

Catch per unit of effort (CPUE) for Atlantic sturgeon (*Acipenser oxyrinchus*) and frequency of tows conducted by depth for the (**A**) National Marine Fisheries Service bottom trawl surveys (NMFS), (**B**) Maine-New Hampshire inshore bottom trawl survey (ME-NH), (**C**) New Jersey Department of Environmental Protection finfish survey (NJDEP), (**D**) New York bottom trawl survey (NYBTS), and (**E**) Massachusetts Division of Marine Fisheries bottom trawl survey (MADMF).

from 5 to 30 m and the majority of the tows occurred within the 10–25 m range (Fig 3B). CPUE was highest for the 10–15 m depth range (0.134 fish/tow) and lowest for 20–30 m range (0.005 fish/tow) (Fig. 3B). A total of 94.78% of all captures occurred in depths less than 20 m (Fig. 3B). CPUE was highest for the winter months (0.124 fish/tow) followed by fall (0.096 fish/tow) and spring (0.079 fish/tow) (Table 1). No Atlantic sturgeon were captured during the summer months (Table 1). During the winter, 74 Atlantic sturgeon were captured of which 67 were captured off northern NJ and of that number, 59 were taken within a small area outside Sandy Hook, NJ. Three fish were captured at 0–20 m depth outside of Delaware Bay, DE. During the fall season, 74 Atlantic sturgeon were captured of which 92% (68 fish) were taken north of Little Egg Inlet, NJ. Of

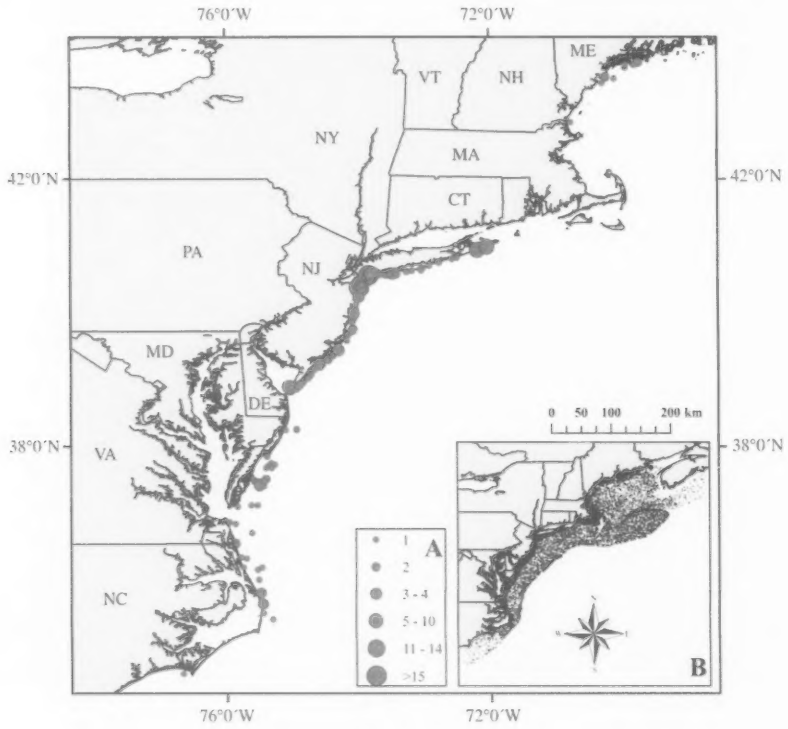

Figure 4

Number of captures of Atlantic sturgeon (*Acipenser oxyrinchus*) from all surveys during spring months. Circle size corresponds to total number of Atlantic sturgeon captured at a given location (insert **A**). Locations of all tows can be seen in insert **B**.

the total Atlantic sturgeon captured, 64% (48 fish) were captured off northern NJ. Captures within the spring occurred along the entire coast of NJ and 44.2% of the captures occurred in Sandy Hook, NJ.

ME-NH inshore bottom trawl survey

A total of 38 Atlantic sturgeon were captured in a total of 1601 bottom trawls from 2001 through 2006 (Table 1). Sampling depths ranged from 10 to 200 m, and three defined peaks in sampling effort occurred at 30 m, 65 m, and 90 m (Fig. 3C). All Atlantic sturgeon were captured between 15 and 90 m depth (Fig. 3C) and 36 of the 38 Atlantic sturgeon were captured near the Kennebec estuarine complex (Fig. 9A). Two additional Atlantic sturgeon were captured south of the Kennebec River, closer to the Saco River.

MADMF bottom trawl survey

Only one Atlantic sturgeon was captured in a total of 5563 bottom trawls (Table 1). Sampling depths ranged from 4 to 86 m, and a peak in sampling effort occurred at a depth of 20 m (Fig. 3D). The only Atlantic sturgeon captured was collected during the spring at a depth of 41 m.

NYBTS

A total of 149 Atlantic sturgeon were captured in 512 random stratified tows (Table 1). Sampling depths ranged from 5 to 35 m and a peak in sampling effort occurred at a depth of 15 m (Fig. 3E). Atlantic sturgeon were captured within all months sampled; however, no Atlantic sturgeon were captured deeper than 20 m. A total of 85% of all Atlantic sturgeon were captured between 5 and 10 m with a mean CPUE of 1.34 (Fig. 3E). CPUE was highest during the fall (0.35 fish/tow) followed by spring (0.33 fish/tow) and summer (0.26 fish/tow) and was lowest during the winter (0.07 fish/tow) (Table 1). Of the 149 Atlantic sturgeon captured, 51% were collected off the western coast of Long Island, 30% were captured off central Long Island, and only one was captured off the east end of Long Island. During the spring, Atlantic sturgeon were captured along the entire coast of Long Island, NY, but 57% were captured off western Long Island, specifically Rockaway, NY. The Rockaway region was also an important area during the fall, accounting for

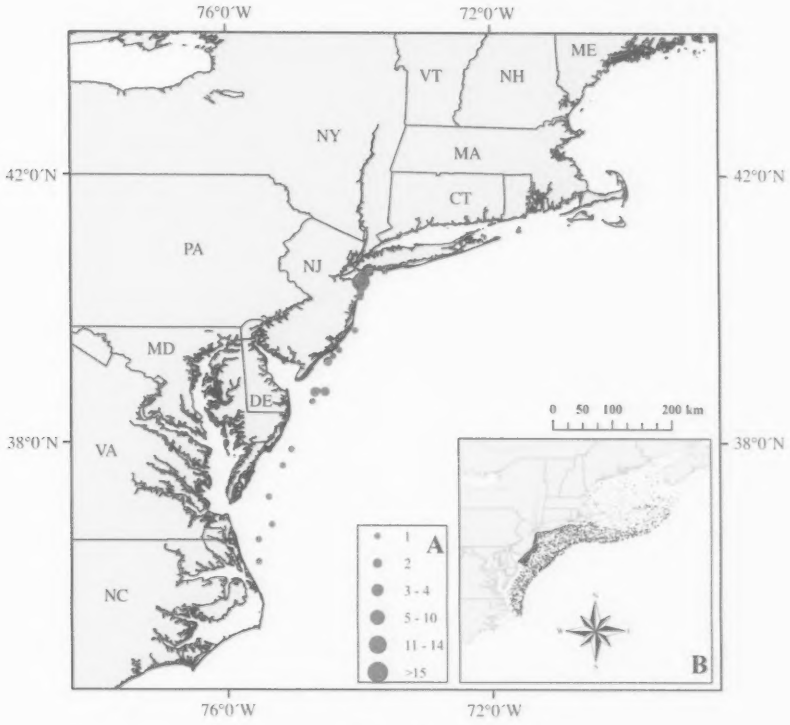

Figure 5

Number of captures of Atlantic sturgeon (*Acipenser oxyrinchus*) from all surveys during winter months. Circle size corresponds to total number of Atlantic sturgeon captured at a given location (insert **A**). Locations of all tows can be seen in insert **B**.

70% of the catches occurring within this region. Twenty-six Atlantic sturgeon were captured in the summer months; 99% were captured in western-central Long Island, NY, and only one was captured along the east end of Long Island. During the winter, all Atlantic sturgeon were captured off the western end of Long Island.

Habitat preferences

Hydrographic variables and distributions of Atlantic sturgeon were compared only for the NMFS bottom trawl survey, NJDEP finfish survey, and for NYBTS for the spring and fall seasons because these contained sufficient Atlantic sturgeon capture data to perform the analyses. The depths (habitat) occupied by Atlantic sturgeon was significantly different from the available depths in the NMFS survey and NYBTS for both the spring and fall surveys and the NJDEP spring survey (Tables 3 and 4). Atlantic sturgeon occupied areas with significantly different temperatures compared to available habitat in the NYBTS spring and NMFS fall survey, as well as areas of significantly different salinities in the NMFS fall and spring surveys and NJDEP spring survey (Table 3). Survey-specific cumulative distribution functions for available and occupied habits with depth, salinity, and temperature profiles are shown in Figure 10 and median values and 95% confidence intervals are listed in Table 4. Where significant differ-

Table 3

P-values from the analysis of habitat preference of Atlantic sturgeon (*Acipenser oxyrinchus*) by season in the northwestern Atlantic Ocean. The fish were captured in the National Marine Fisheries Service (NMFS) bottom trawl survey, New Jersey Department of Environmental Protection (NJDEP) finfish survey, and New York bottom trawl survey (NYBTS). Bold font indicates a significant difference ($P<0.01$) between Atlantic sturgeon habitat preference and the available habitat.

Season	Survey	Depth	Temperature	Salinity
fall	NMFS	<0.005	<0.005	<0.005
fall	NJDEP	0.129	0.173	0.273
fall	NYBTS	<0.005	0.518	0.530
spring	NMFS	<0.005	0.355	0.001
spring	NJDEP	<0.005	0.173	<0.005
spring	NYBTS	<0.005	0.001	0.084

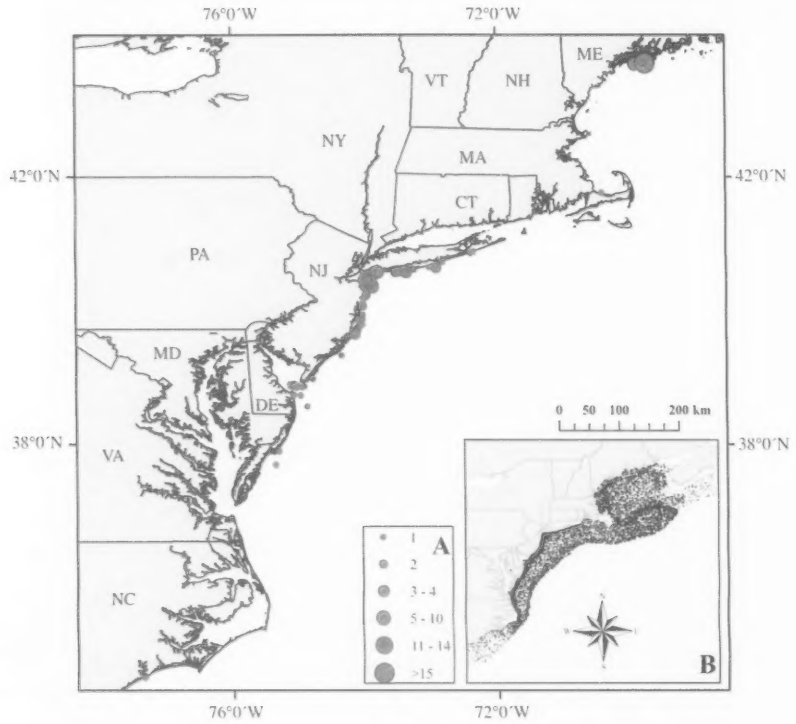

Figure 6

Number of captures of Atlantic sturgeon (*Acipenser oxyrinchus*) from all surveys during fall months. Circle size corresponds to total number of Atlantic sturgeon captured at a given location (insert **A**). Locations of all tows can be seen in insert **B**.

ences in depth occurred, Atlantic sturgeon were always found in shallower water than in potentially available habitat (Table 4, Fig. 10). Salinities of occupied areas were less than those of available habitat in all surveys, although only the NMFS fall and spring survey and NJDEP spring survey had significant differences (Table 4, Fig. 10). In two circumstances the temperature of occupied habitat was significantly warmer than that of available habitat, whereas temperature for the other seasons and surveys showed no trend (Table 4, Fig. 10).

Discussion

A majority of the Atlantic sturgeon captured along the continental shelf from ME to NC were juveniles aggregating in specific locations around the mouths of estuarine complexes and along narrow dispersal corridors in shallow water (<20 m) from Cape Hatteras (NC) to the southern tip of Long Island (NY). The highest catches occurred within the NY Bight in water 10–15 m deep, particularly during the spring and fall. Few sturgeon were captured north of MA. Little work has been done to describe the marine habitat distribution and habitat preference of Atlantic sturgeon, but similar coast-wide, shallow (with respect to regional bathymetry) marine distributions have been shown for green sturgeon (*Acipenser medirostris*) (Erickson and Hightower, 2007) and Gulf sturgeon (*Acipenser oxyrinchus desotoi*) (Edwards et al., 2007; Ross et al., 2009). The shallow, coast-wide habitat identified within this study is also consistent with Atlantic sturgeon bycatch data (Stein et al., 2004a, 2004b). Our comprehensive analysis of a coast-wide collection of surveys revealed the area between the NY Bight to VA as a region of overwintering habitat for juvenile Atlantic sturgeon. This finding agrees with that of Laney et al. (2007), who found the coastal waters off NC and VA to be important overwintering habitat for Atlantic sturgeon. Atlantic sturgeon that originated from the Hudson River represented 43.5% of those in the NC overwintering habitat (Laney et al., 2007) a percentage that agrees with Dovel and Berggren's (1983) tagging data that revealed a southerly movement of Atlantic sturgeon from the Hudson River. In addition to Laney et al. (2007), there have been further reports of Atlantic sturgeon in marine waters off the coast of South Carolina during winter months (Collins and Smith, 1997). The identification of the NY Bight as an important overwintering area has not been widely reported; therefore determining the

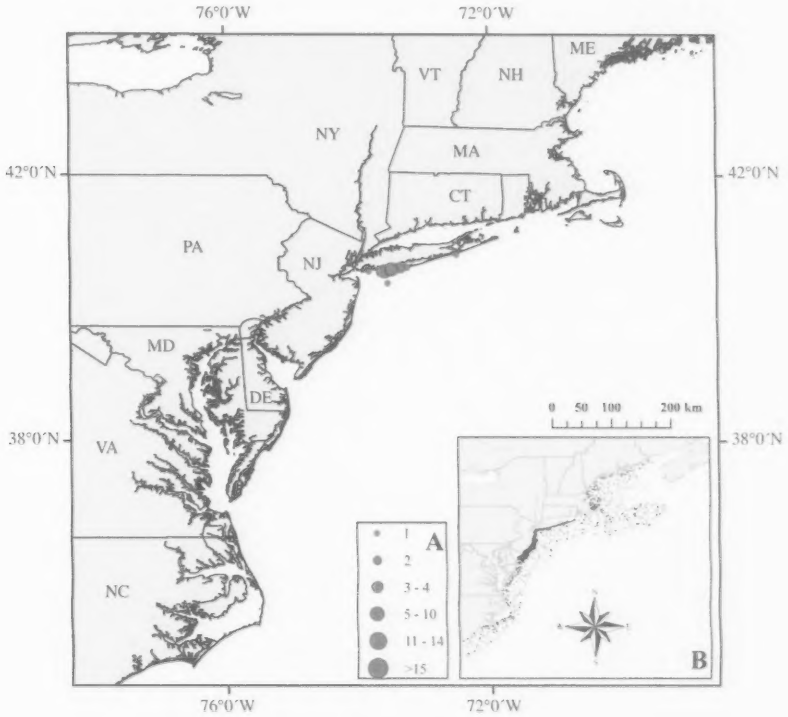

Figure 7

Number of captures of Atlantic sturgeon (*Acipenser oxyrinchus*) from all surveys during summer months. Circle size corresponds to total number of Atlantic sturgeon captured at a given location (insert **A**). Locations of all tows can be seen in insert **B**.

genetic makeup of the sturgeon in this area would add important information on Atlantic sturgeon demographics and movements.

Atlantic sturgeon had a coast-wide distribution during the spring and fall, and southerly and centrally located distributions during the winter and summer, respectively. These results corroborate tagging data that indicate that Atlantic sturgeon undergo large-scale southerly fall migrations and northerly spring migrations (Dovel and Berggren, 1983). Catches varied by season, but were greatest during the fall and spring months. Because of the strong seasonal movements of Atlantic sturgeon, the timing of surveys is critical for observing movement patterns.

Interaction of Atlantic sturgeon abundance with temporal and spatial variability in sampling effort

Some of the variation in distribution and abundance of Atlantic sturgeon can be explained by temporal and spatial differ-

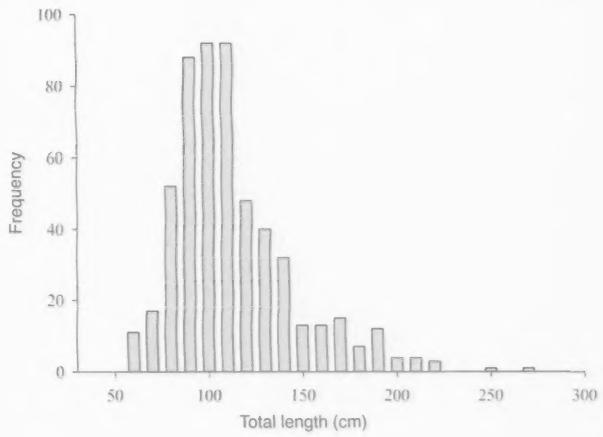

Figure 8

Total length distribution for Atlantic sturgeon (*Acipenser oxyrinchus*) captured in all surveys combined.

ences in sampling effort. Stein et al. (2004a) reported that MA ports have one of the highest cumulative catches of Atlantic sturgeon. This high rate contrasts with that for the MADMF bottom trawl survey, during which virtually no Atlantic sturgeon were captured. The discrepancy between reports of Atlantic sturgeon in MA waters likely comes from the timing of sampling. Stein et al. (2004a) showed the highest bycatch rates in June and November for bottom trawl fisheries, whereas the MADMF survey took place during May and September. Any aggregations and dispersal of Atlantic sturgeon within MA marine waters may occur at spatial and temporal scales that are missed by the survey. The absence of Atlantic sturgeon during the MADMF survey does, however, indicate lower abundance within the area surveyed during comparable time frames because Atlantic sturgeon are captured at relatively high rates by other surveys during this period. More work should be done to monitor Atlantic sturgeon habitat during other months not typically sampled by the MADMF survey because it is possible that Atlantic sturgeon are present in higher concentrations during months that are not routinely sampled.

The NMFS survey missed critical areas for Atlantic sturgeon because inshore areas in certain regions could not be sampled. Such areas include important overwintering habitat identified within this study in NY waters and by Laney et al. (2007) in VA and NC waters, in addition to critical habitat within the GOM. The ME-NH inshore bottom trawl survey was used to identify the Kennebec estuarine complex as an important concentration area for Atlantic sturgeon within the GOM region because shallower areas are sampled with this survey. During additional inshore surveys, such as the Northeast Fisheries Sciences Center (NEFSC) industry-based surveys for cod (*Gadus morhua*) and yellowtail (*Limanda ferruginea*), Atlantic sturgeon have been captured between the Saco and Kennebec rivers in fall, winter, and spring (Fig. 9A; W. Kramer, personal commun.[5]). Stein et al. (2004a, 2004b) also showed that Atlantic sturgeon are captured as bycatch within this region in sink gillnets. The depth distribution of Atlantic sturgeon within the GOM was deeper than that for the other coast-wide captures, but similar to those reported for green sturgeon (Erickson and Hightower, 2007) in that both species occupied areas of shallow depth in relation to the bathymetric characteristics of the region. There has not been sufficient inshore trawling conducted during the winter and summer to validate whether the GOM is important year-round habitat.

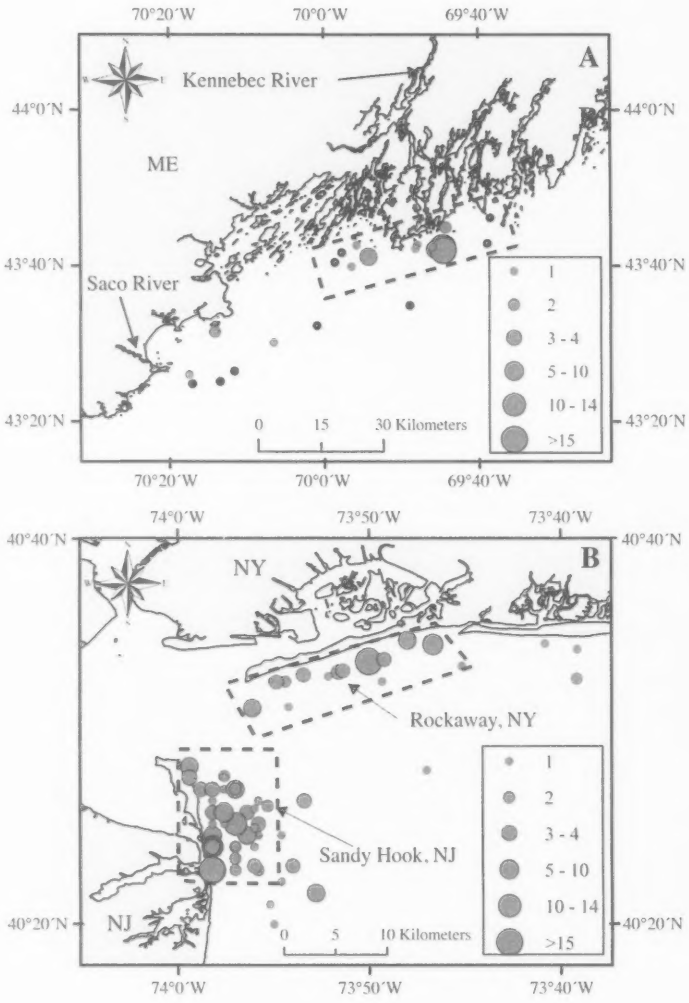

Figure 9

Number of captures of Atlantic sturgeon (*Acipenser oxyrinchus*) determined from (**A**) the Gulf of Maine from the Maine-New Hampshire bottom trawl surveys (gray circles) and from the Northeast Fisheries Science Center industry-based surveys for cod (*Gadus morhua*) and yellowtail (*Limanda ferruginea*) (black circles) and (**B**) Sandy Hook, NJ and Rockaway NY, including all captures from the National Marine Fisheries Service bottom trawl survey, New Jersey Department of Environmental Protection finfish survey, and New York bottom trawl survey. Dotted lines in both panels represent suggested closed areas for habitat protection. Note different scales in figure.

[5] Kramer, William. 2009. NOAA Fisheries Service, Ecosystems Survey Branch, 166 Water St., Woodshole, MA 02543.

Table 4

Median and 95% confidence intervals for available and occupied habitat of Atlantic sturgeon (*Acipenser oxyrinchus*) for depth, temperature, and salinity for the fall and spring National Marine Fisheries Service bottom trawl survey (NMFS), New Jersey Department of Environmental Protection finfish survey (NJDEP), and New York bottom trawl survey (NYBTS) where "available habitat" represents all habitat sampled and "occupied habitat" represents habitat where Atlantic sturgeon were captured.

Season	Parameter	Survey	Median	95% confidence interval
Fall	Depth (m)	NMFS available habitat	76.0	15.5–260.5
		NMFS occupied habitat	18.0	10.0–25.0
		NJDEP available habitat	19.0	8.0–27.0
		NJDEP occupied habitat	16.0	7.0–22.0
		NYBTS available habitat	23.8	9.5–30.3
		NYBTS occupied habitat	10.7	9.0–17.0
	Temperature (°C)	NMFS available habitat	10.6	5.9–22.5
		NMFS occupied habitat	18.9	13.3–23.3
		NJDEP available habitat	15.8	12.3–18.6
		NJDEP occupied habitat	14.8	13.3–17.6
		NYBTS available habitat	15.3	13.5–19.3
		NYBTS occupied habitat	16.8	13.6–19.9
	Salinity (ppt)	NMFS available habitat	33.1	31.0–35.4
		NMFS occupied habitat	31.6	29.3–32.0
		NJDEP available habitat	32.0	29.6–33.5
		NJDEP occupied habitat	31.5	29.5–33.1
		NYBTS available habitat	31.4	30.1–32.9
		NYBTS occupied habitat	31.3	29.4–31.8
Spring	Depth (m)	NMFS available habitat	76.0	16.0–259.0
		NMFS occupied habitat	18.0	8.0–27.0
		NJDEP available habitat	19.0	7.5–27.0
		NJDEP occupied habitat	12.0	7.0–18.0
		NYBTS available habitat	22.4	9.9–29.7
		NYBTS occupied habitat	9.9	9.9–13.9
	Temperature (°C)	NMFS available habitat	6.0	3.4–12.5
		NMFS occupied habitat	6.4	3.2–15.0
		NJDEP available habitat	9.1	4.9–18.8
		NJDEP occupied habitat	11.0	5.7–19.0
		NYBTS available habitat	9.4	5.1–14.6
		NYBTS occupied habitat	11.1	5.7–13.9
	Salinity (ppt)	NMFS available habitat	33.2	31.4–35.4
		NMFS occupied habitat	32.0	27.0–32.8
		NJDEP available habitat	32.0	30.0–34.0
		NJDEP occupied habitat	30.0	28.8–35.0
		NYBTS available habitat	31.6	30.2–33.1
		NYBTS occupied habitat	30.9	29.9–32.3

Although the NMFS survey covered the entire continental shelf, no fish were captured deeper than 30 m. However, Atlantic sturgeon of unknown size have been captured in deeper waters (>100 m) on the continental shelf as bycatch in gillnet fisheries (Stein et al. 2004b; ASMFC[6]). Additionally, there have only been two recorded trawl captures of an Atlantic sturgeon in deep waters; one mature Atlantic sturgeon (225 cm) was captured in the Hudson canyon in water 110 m deep off NY and NJ and another was captured in Wilmington Canyon, 113 km southeast of Atlantic City, NJ (Timoshkin, 1968). The lack of trawl-caught fish on the continental shelf may be a result of either a gap in timing of the sampling and Atlantic sturgeon migrations on or off the shelf, a function of gear selectivity towards smaller

[6] ASMFC (Atlantic States Marine Fisheries Commission). 2007. Estimation of Atlantic sturgeon bycatch in coastal Atlantic commercial fisheries of New England and the Mid-Atlantic, 95 p. ASMFC,Washington D.C.

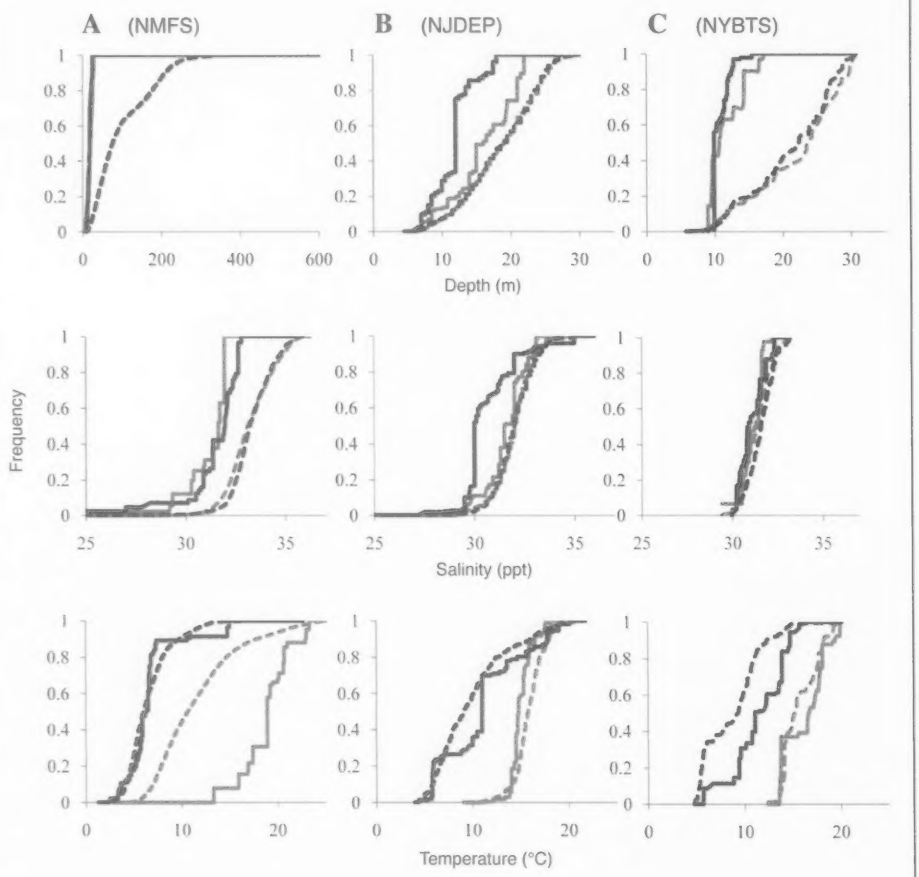

Figure 10

Cumulative distribution functions for available habitat and habitat occupied by Atlantic sturgeon (*Acipenser oxyrinchus*) in the fall and spring surveys for (**A**) National Marine Fisheries Service bottom trawl surveys (NMFS), (**B**) New Jersey Department of Environmental Protection finfish survey (NJDEP), and (**C**) New York bottom trawl survey (NYBTS) for depth (m), salinity (ppt), and temperature (°C). Solid lines indicate habitat occupied by *A. oxyrinchus* (gray=fall; black=spring) and dashed lines indicate available habitat (dashed gray=fall; dashed black=spring).

fish, or simply a scarcity of Atlantic sturgeon. Either a substantial increase in trawl survey effort or the use of different gears, such as gillnets, may be required in order to capture Atlantic sturgeon along the shelf.

Essential fish habitat

The Magnuson-Stevens Fishery Conservation and Management Act requires identification of Essential Fish Habitat (EFH), defined as waters or substrate used for spawning, breeding, feeding or growth to maturity, in order to minimize adverse effects of fishing and to promote conservation and enhancement of such habitat for particular species. Unfortunately, EFH can only be defined for federally managed species and does not include species such as Atlantic sturgeon which are managed by regional fishery management councils. Atlantic sturgeon is a current candidate species for listing under the US Endangered Species Act, and if listed, the identification of critical habitat necessary to recover the species will be required. The identification of critical habitat for listed species is mandatory and is defined as all areas essential to the conservation of the species. Without EFH or critical habitat designation, habitat degradation and incidental mortality within critical areas will continue to hinder population recovery.

Our analysis of habitat preferences indicated that depth was the primary environmental characteristic defining the Atlantic sturgeon distribution. Thus, es-

sential habitat for juvenile marine migrant Atlantic sturgeon can broadly be defined as coastal waters <20 m depth, and it is concentrated in areas adjacent to estuaries such as the Hudson River–NY Bight, Delaware Bay, Chesapeake Bay, Cape Hatteras, and Kennebec River. This narrow band of shallow water appears to represent an important habitat corridor and potential migration path. There are likely additional hotspots along the migration corridor, but greater temporal and spatial sampling effort is required to identify them. Other authors have reported concentrations of Atlantic sturgeon in Long Island Sound (Bain et al., 2000; Savoy and Pacileo, 2003) and NC (Laney et al., 2007), and Stein et al. (2004a) reported several concentrations of Atlantic sturgeon in Massachusetts Bay, RI, NJ, and DE. However, Stein et al. (2004a) used bycatch data in areas where captures were lowest during the summer months while the fishing rates were highest. However, this change in fishing effort may influence the observed distributions.

The reason(s) for aggregations of Atlantic sturgeon migrants are not understood, nor are their movements to and from aggregation areas. Concentrations identified by Stein et al. (2004b) led the authors to suggest that temperature, bathymetry, geomorphic formations, food habits, and the sampling gear type used may contribute to observed movements and aggregation of Atlantic sturgeon. Complex water circulation patterns are also a potential reason for observed concentrations of Atlantic sturgeon (Wilk and Silverman, 1976; Savoy and Pacileo, 2003). Hatin et al. (2002) found that Atlantic sturgeon concentrated within the St. Lawrence estuary had large numbers of nematodes and oligochaetes within their stomachs, which would indicate that these habitats are feeding areas. Known seasonal migrations often involve energetic demands related to food availability, environmental factors, and reproductive activity (Roff, 2002). Because the majority of captures are juveniles, reproductive activity is not a likely cause for movement, although causal mechanisms influencing traits under selection are difficult to identify because life-history stages are often linked through long-term fitness (Taborsky, 2006). We hypothesize that migrations are depth restricted and aggregations are related to food availability, and that seasonal cues, temperature in particular, drive movement.

Current and future management of Atlantic sturgeon

Current knowledge indicates that the majority of Atlantic sturgeon populations have been extirpated and that the Hudson River stock is one of the largest remaining populations (Waldman et al., 1996; van Eenennaam et al., 1998; Savoy and Pacileo, 2002; Secor et al., 2002). Three fishery management tools commonly used to help restore depleted populations are 1) minimum size limits, 2) temporary closures of the fishery, and 3) marine reserves (Nowlis, 2000). Management of Atlantic sturgeon has been accomplished by minimum size limits since the early 1990s, followed directly by a 40-year complete closure of the fishery beginning in 1998. Currently, after 10 years of the fishery closure, recruitment within the Hudson River still remains at historic lows (Kahnle et al., 2007).

Because previous Atlantic sturgeon management has not resulted in significant improvements to populations, recovery efforts should now focus on establishing marine reserves or implementing area closures to protect essential habitat and to reduce fishing mortality on juveniles (Collins et al., 2000). Specifically, Sandy Hook (NJ), Rockaway (NY), and Kennebec (ME), which are hotspots of Atlantic sturgeon captures, as identified by this study, should be protected. Although sturgeon are not as abundant in the Kennebec region in ME as in NY and NJ waters, this region represents a unique hotspot. It is of particular importance because Atlantic sturgeon captured in ME river systems have been shown to represent a separate discrete population segment (Grunwald et al., 2008). The genetic origins of the Atlantic sturgeon captured within marine waters of ME are unknown, but they are likely to originate from multiple stocks. Because of the proximity of ME river systems, it is probable that the majority of these Atlantic sturgeon are part of this discrete population segment. If our recommended habitat protection were to occur, the total amount of closed area within these locations would be relatively small—totaling 85.47 km^2 within NJ (Fig. 9A), 106.19 km^2 within NY (Fig. 9A), and 209.79 km^2 within ME (Fig. 9B). In addition, although Atlantic sturgeon are highly migratory, primary juvenile habitat and migrations are limited to narrow corridors in waters less than 20 m deep. The presence of Atlantic sturgeon in such narrow bands of water indicates a seasonal or permanent closure to gillnet and trawl fisheries could be successful. By focusing immediate efforts on the protection of these hotspots and corridor pathways, bycatch mortality will be reduced effectively through protection of habitat. Further efforts should also be made to protect important areas within other systems and to conserve the several discrete population segments defined by ASSRT[3] and Grunwald et al. (2008) and to promote genetic diversity among Atlantic sturgeon populations.

By understanding the time periods of localized aggregations and movements of Atlantic sturgeon, plans could be developed that minimize the extent and length of closures that are concentrated within narrow corridors. Some states already restrict inshore trawling which limits fishery interactions with Atlantic sturgeon, such as NJ (3.22 km limit), MD (1.61 km limit), DE (no trawling), and NY (various no trawl zones in marine waters). Any spatial closures require proper enforcement and substantial community-level support for successful implementation (Sumaila et al., 2000). Although broad-scale movement patterns are becoming clearer, work is required to understand the finer scale movements of Atlantic sturgeon such that any spatial management plans could be minimized while still achieving adequate protection. Current plans toward

understanding finer-scale movements are aided by cooperative efforts such as those of the Atlantic Cooperative Telemetry (ACT) network, which is a large scale collaborative telemetry network of ~30 groups from Maine to South Carolina (D. Fox and T. Savoy, personal commun.[7,8]). Such coordinated efforts are steps in the right direction for species conservation. Once fine-scale movements are understood, in particular for aggregation areas, fishery managers will be better informed as to how to limit interactions between fisheries and the near-endangered Atlantic sturgeon while minimizing economic impacts. Improving estimates of fishery bycatch mortality would be of enormous value, in particular if these estimates included a spatial perspective. Regardless of the outcome of the current consideration of Atlantic sturgeon for listing under the endangered species act, a coordinated effort among academic, federal, state, and local institutions will be required to conserve this ancient species.

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Day and night abundance, distribution, and activity patterns of demersal fishes on Heceta Bank, Oregon

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Abstract—Most shallow-dwelling tropical marine fishes exhibit different activity patterns during the day and night but show similar transition behavior among habitat sites despite the dissimilar assemblages of the species. However, changes in species abundance, distribution, and activity patterns have only rarely been examined in temperate deepwater habitats during the day and night, where day-to-night differences in light intensity are extremely slight. Direct-observation surveys were conducted over several depths and habitat types on Heceta Bank, the largest rocky bank off the Oregon coast. Day and night fish community composition, relative density, and activity levels were compared by using videotape footage from a remotely operated vehicle (ROV) operated along paired transects. Habitat-specific abundance and activity were determined for 31 taxa or groups. General patterns observed were similar to shallow temperate day and night studies, with an overall increase in the abundance and activity of fishes during the day than at night, particularly in shallower cobble, boulder, and rock ridge habitats. Smaller schooling rockfishes (*Sebastes* spp.) were more abundant and active in day than in night transects, and sharpchin (*S. zacentrus*) and harlequin (*S. variegatus*) rockfish were significantly more abundant in night transects. Most taxa, however, did not exhibit distinct diurnal or nocturnal activity patterns. Rosethorn rockfish (*S. helvomaculatus*) and hagfishes (*Eptatretus* spp.) showed the clearest diurnal and nocturnal activity patterns, respectively. Because day and night distributions and activity patterns in demersal fishes are likely to influence both catchability and observability in bottom trawl and direct-count *in situ* surveys, the patterns observed in the current study should be considered for survey design and interpretation.

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For surveys of groundfish, swept-area trawls are generally conducted and direct-counts from video cameras are recorded during daylight hours (Gunderson, 1993; Adams et al., 1995; Yoklavich et al., 2000; Wakefield et al., 2005). If activity patterns vary among species during the day versus the night, conclusions about relative abundance, community composition, and habitat affiliations could be incomplete or biased. It is not known whether diel activity and abundance patterns in fishes commonly found in shallow temperate and tropical areas are similar for fishes inhabiting deeper temperate areas along the west coast of North America, where diel changes in light levels are subtle. We used a repeat-transect (the transect was followed once during the day and again at night) visual sampling survey to examine differences in fish abundance, distribution, and behavior on Heceta Bank, a temperate reef and ridge ecosystem off the central coast of Oregon.

Diel distributions and activity patterns in fishes have been well studied in tropical areas, and these studies have shown that most fishes exhibit distinct diel behavioral patterns (Collette and Talbot, 1972; Hobson, 1972; Helfman, 1978). Generally, two-thirds of fishes are diurnal, one-third are nocturnal, and a marked change in the vertical distribution of fishes occurs between day and night (Helfman, 1978). Most fishes rigidly follow a diurnal or nocturnal activity pattern, exhibiting very low activity in shelter-providing areas and high activity during feeding. Rotation between ecological niches at daytime and at night, such as the broad replacement of diurnal planktivores with predators during the night, proceeds in predictable patterns (Hobson, 1972). Some of the largest schools encountered by day in tropical waters are nonfeeding, resting schools of nocturnal fishes, and many diurnal fishes actively school in the water column by day and then rest individually at night (Hobson and Chess, 1973; Parrish, 1992).

Although not as well studied, diel shifts in fish communities and behavioral patterns in shallow temperate habitats are less distinct than

those observed in warmer water regions (Hobson et al., 1981). Deepwater habitats with low light penetration would therefore be expected to show only subtle changes in species composition, densities, or activities during night hours. Nevertheless, diel distributions and activity patterns of some species of fish have been observed in temperate areas at substantial depths. On Stonewall Bank, Oregon, *in situ* direct observations in shelf waters (41–70 m) revealed that species composition changed little from day to night, but the abundance of some fishes decreased dramatically (Hixon and Tissot[1]). Specifically, juvenile rockfishes (*Sebastes* spp.) and rosethorn rockfishes (*S. helvomaculatus*) showed much greater abundance during the day, and spotted ratfish (*Hydrolagus colliei*) and widow rockfish (*S. entomelas*) were significantly more abundant at night. Within Pribilof Canyon (181 to 240 m) in the Bering Sea, Pacific ocean perch (*S. alutus*) actively fed on euphausiids just above sea-whip "forests" during the day and were observed to be less active within the sea-whip habitat at night (Brodeur, 2001). In deeper rocky bank areas with lower levels of ambient light, it is not known whether an overall change from high to low activity from day to night exists, as is observed in shallow temperate fish communities (Ebeling and Bray, 1976; Hobson and Chess, 1976; Moulton, 1977).

We hypothesized there would be differences in the day and night assemblages of fishes in deep temperate waters, but that the patterns and changes in abundance and activity would be less distinct than those observed in tropical and shallow temperate fish communities. Given its diverse range of habitats and water depths, Heceta Bank is an ideal location for studying day-night patterns of demersal fishes among different depths and habitat types.

Materials and methods

Study area

Heceta Bank is one of the largest of all submarine, rocky banks off the west coast of the United States, located approximately 60 km off the central Oregon coast, extending 50 km north to south (Fig. 1). The bank has been a primary focus of direct-observation studies of groundfishes, invertebrates, and habitat since the late 1980s (Pearcy et al., 1989; Stein et al., 1992; Wakefield et al., 2005; Whitmire et al., 2007; Hixon and Tissot[1]; Hixon et al.[2]). This bank comprises a wide range of benthic habitats from rock ridge and boulder to sand, and mud and extends from 70 m depth at the top of the bank to >500 m in water depth on its flanks (Figs. 1 and 2). The bank has been generally characterized as having three major habitat-depth profiles: 1) shallow rock ridge and boulder habitat from 70 to 100 m; 2) boulder and cobble habitat at mid-depth from 100 to 150 m; and 3) mud habitat in greater than 150 m of water depth (Hixon et al.[2]). Some portions of the bank show great habitat variability (Hixon and Tissot[1]).

Light levels

Ambient light levels on Heceta Bank were measured two weeks before the current study by the Plankton/Bio-Optics group at Oregon State University during a Global Ocean Ecosystems Dynamics (GLOBEC) study of meso- and fine-scale physical and biological fields (Whitmire and Cowles, unpubl. data[3]). In order to characterize the underwater light environment over the bank, the OSU group used *in situ* total absorption coefficient data. Absorption measurements (a_t[488 nm]) were collected with a dual-path absorption and attenuation meter (ac-9; WET Labs, Inc., Philomath, OR) that was mounted on a SeaSOAR, a towed undulating vehicle used to deploy a wide range of oceanographic monitoring equipment, and towed in an undulating fashion along east to west track lines over the bank during daylight hours on 5 and 6 June 2000. One percent light levels (in relation to surface light values), a commonly used oceanographic parameter for comparing light attenuation, were reached at approximately 20 m in high chlorophyll coastal waters (~3 to 6 mg/m), and at approximately 50 m in waters at the western end of the east–west transects. This empirical approach for light attenuation agreed well with theoretical relationships between depth and light attenuation as applied to coastal and offshore waters within the California Current (Morel, 1988; Barnard et al., 1999).

Survey transects

From 19 to 26 June 2000, an interdisciplinary group of scientists used the remotely operated vehicle (ROV) *ROPOS* (Remote Operated Platform for Ocean Science), managed and operated by the Canadian Scientific Submersible Facility (CSSF), to revisit five stations on Heceta Bank that were established in the 1980s (Figs. 1 and 2) (Pearcy et al., 1989; Stein et al., 1992; Hixon and Tissot[1]; Hixon et al.[2]) and to explore new sites on the bank. At each of five historical stations fish assemblages were compared between day and night.

The ROV *ROPOS* is well suited for deepwater demersal fish surveys. *ROPOS* is a 30-horsepower electrohydraulic ROV equipped with two video systems, a

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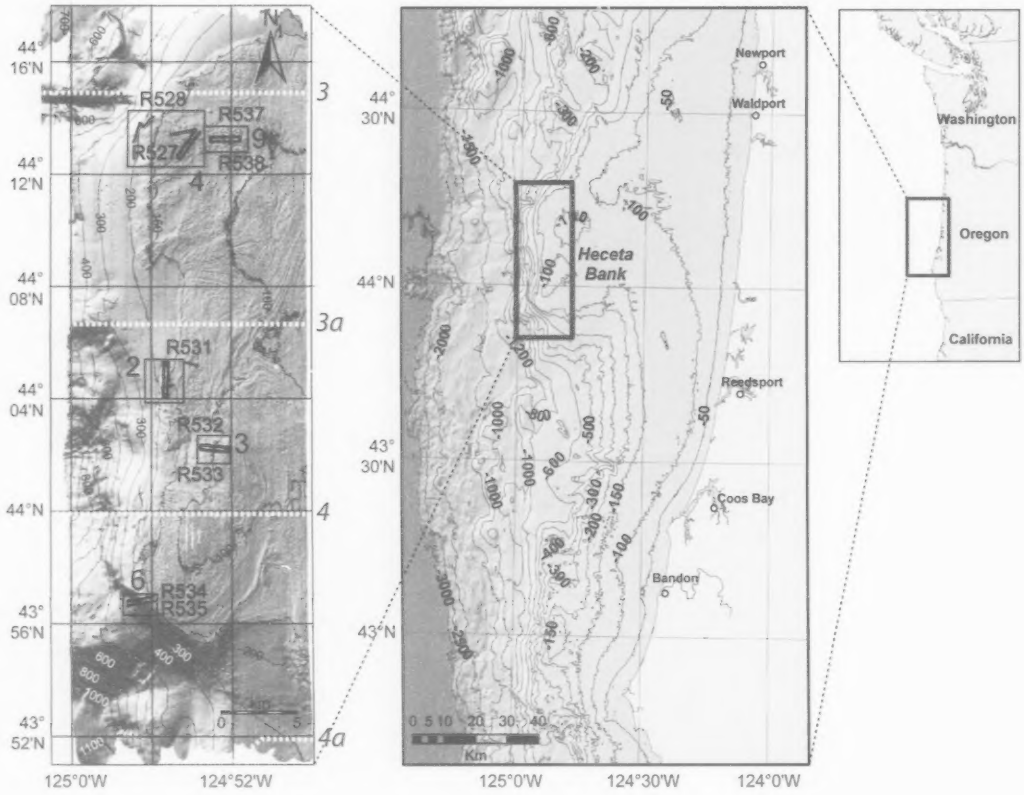

Figure 1

Location and depth (in meters) of the study area, Heceta Bank off the Oregon coast, and the area mapped with a multibeam sonar system in 1998 (MBARI 2201; modified from Whitmire et al., 2008). The leftmost panel shows the location of the ROV transects for areas surveyed during day and night periods for each station (boxes) on Heceta Bank, Oregon. Global Ocean Ecosystem Dynamics (GLOBEC) track lines for light levels (lines 3, 3a, 4, and 4a) are shown in white dashed lines and are labeled to the right of the map. Depth contours are given in meters.

broadcast-quality Sony DXC 950 three-chip color video camera (used for fish and habitat video analysis), a wide-angle low light black and white video camera, an obstacle avoidance sonar, a compass, three arc lights (250 W), four halogen lights with adjustable intensity (250 W), and a 10-hp cage with a separate light and video system (Wallace and Shepherd, 2003). One pair of scaling lasers (10-cm scale) mounted in parallel on the color video camera provided scale in the field of view of the video image for estimating the width of transects and the size of fishes and features on the seafloor. The distance surveyed was determined from smoothed navigation of tracklines obtained from ultra-short baseline tracking. Real-time audio commentary of habitat type and fish identification was overlaid on the videotape. The technical side of the ROV dive transects was managed and conducted by two four-member CSSF teams that worked in alternating 12-hour watches. Parallel interdisciplinary science teams worked in tandem with the ROV group to direct the scientific operations and ensure consistency in sampling effort.

Day and night complements were completed outside the two-hour twilight periods of dawn (0436 to 0636 PST) and dusk (2006 to 2206 PST) to avoid possible biases due to changes in the behavior of fishes during crepuscular periods (Yoklavich et al., 2000). Only daytime fish transects that overlapped geographically with, or were in close proximity to, corresponding night fish transects (stations 2, 3, 4, 6, and 9) were used in this analysis. Station 4 contained a night transect located approximately 1 nautical mile (nmi) away from the day transect but in a comparable depth range and over similar habitat, and therefore it was included in the analysis.

A total area of 5.5 hectares along a combined total transect distance of 40.9 km was surveyed during 45.6 hours (Fig. 2). Stations varied in habitat composition and depth (Fig. 2). Shallow areas (70–100 m) were dominated

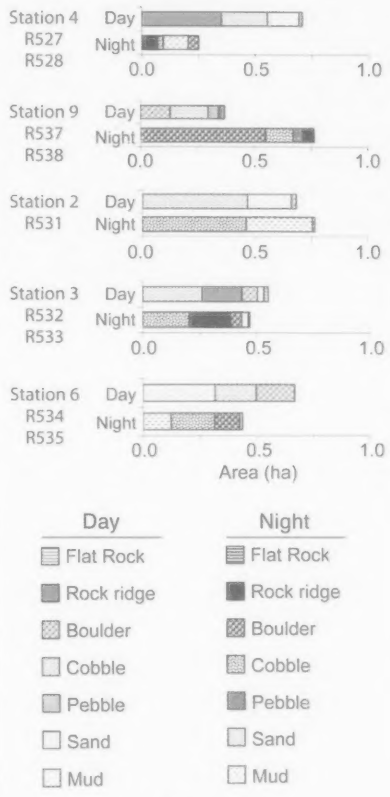

Figure 2

Bar graphs indicate the area and relative composition (in hectares) of each primary habitat surveyed along transects during day and night periods for each station on Heceta Bank, OR. ROV dives associated with each station are identified by an "R" followed by the dive number.

by rock ridge and boulder, mid-depth by cobble, and deeper areas by mud habitat with isolated patches of cobble and boulder. Rock ridge, boulder, cobble, and mud composed the four most dominant primary habitat types.

Videotape analysis

Videotape collected along all transects was analyzed for fish and habitat identification. Sunset, dawn, dusk, and nautical twilight times (Pacific daylight savings time) were derived from the U.S. Naval Observatory website (http://www.usno.navy.mil/, accessed June 2000) and calculated for the day of each dive by using the specific longitude and latitude coordinates (degrees and minutes) for each station.

Transects were subdivided into habitat patches, based on primary habitat types observed on the videotapes. Seafloor habitats were classified into seven standardized categories (Hixon and Tissot[1]; Stein et al., 1992): rock ridge (high relief where vertical rock was found to be >3.0 m); flat rock (low relief where vertical rock was found to be ≤3.0 m); boulder (300–25.6 cm rock); cobble (25.6–6.4 cm rock); pebble (6.4–0.2 cm rock); sand (2.0–0.06 mm); and mud (<0.06 mm). Only the primary habitat (≥50% of the seafloor) in the field of view was used in our analysis. The length of each habitat patch was determined by using the geographic position recorded at the start and end of each patch. With the scaling lasers, the width of each transect was estimated by selecting random frames every minute during each transect, measuring the width of these lasers on the video monitor, and extrapolating to the field of view. Transect width ranged from 1.3 to 2.1 meters. The area of each patch was determined by multiplying the patch length by the average patch width. Each transect consisted of a few to many habitat patches, depending on the variability of substrate.

Videotape analysis was performed by two technicians simultaneously in order to confirm fish identifications, counts, and fish activity. All fishes were identified to the lowest practical taxonomic unit (usually to species) and total fish length was estimated to the nearest 5 cm. For fish that could be identified to a taxonomic group, but not species, a generalized abbreviation was used (e.g., FF for unidentified flatfish), and in cases where the fish observed was one of two species, a new abbreviation was created to accommodate this situation. Fish were counted at the point where they passed through the level of the scaling lasers and were assigned a GMT time that became a permanent time and geographic reference point in a database. A single anatomical feature (eye) was used to determine whether or not a fish was considered within the transect to prevent underestimating transect width and overestimating abundance. We restricted our analysis to 31 identified species or taxonomic groups that were seen frequently enough to represent ≥0.1% of the total day and night fish density (number of fish per hectare). Exceptions to this rule were the inclusion of three rarely seen species: darkblotched rockfish (*S. crameri*), because this is an important commercial species; kelp greenling (*Hexagrammos decagrammus*); and bigfin eelpout (*Lycodes cortezianus*), because the day-night activity patterns of the latter two have been studied in shallow temperate areas (Moulton, 1977). Some categories of multiple taxa were created, such as "pygmy-Puget Sound rockfish complex" (*S. wilsoni* and *S. emphaeus*), where it was impossible to identify every individual in aggregations. Another common category was "unidentified rockfish," where it was not possible to classify a rockfish to species conclusively. "Unidentified juvenile rockfish" (abbreviation RRF) were categorized by size (<10 cm long), not by morphological features, because video resolution and inherent difficulty of *in situ* identification of young-of-the-year rockfishes precludes determinations at the level of species. Hagfishes (*Eptatretus* spp.) were not identified to species, but on the basis of depth of

occurrence, the species observed was probably the Pacific hagfish (*Eptatretus stoutii*) (Barss, 1993).

All fish in the videotapes were counted and assigned an activity category ("active" or "inactive"). The two categories were developed in order to analyze the videotape efficiently and quantitatively, and all fishes were placed into one of the two categories. Active fish were off the bottom (or temporarily in contact with the substrate), and inactive fish were in contact with the substrate (e.g., in contact with the seafloor or were occupying crevices). All flatfish were excluded from the activity analysis because of our definition of "activity." We assumed that fish were counted only once and that the submersible did not influence the activity of fishes. When the ROV clearly affected the behavior of a fish, the activity of the fish observed before the ROV interruption was used in analyses.

Data analysis

Relative abundance was determined for each taxon on a broad scale over all stations (2, 3, 4, 6, and 9) and all habitat types, and on a finer scale within each of the four primary habitat types (rock ridge, boulder, cobble, and mud) over all stations. Fish abundance was first normalized by dividing the abundance for a given taxon in a habitat patch by the area swept in that habitat patch. Relative abundance in a daytime habitat patch was matched up with a relative abundance in a nighttime habitat patch of closest geographic proximity for a given taxon. These pairs were used to create the ranks in a Wilcoxon signed-rank test. For all taxa, 402 habitat patches were included in the analysis, and an average of 59 habitat patches were compared for each taxon (many taxa were in the same habitat patch). This enabled us to estimate if relative abundance trends were consistent at both scales. For the finer scale, some habitat types (e.g., flat rock) did not contain sufficient relative abundance for analysis.

The Wilcoxon signed-rank test was performed with S-Plus, vers. 3.2 software (TIBCO Software Inc., Palo Alto, CA) to determine significant differences in the activity of fishes during day and night (Ramsey and Schafer, 2002). This test involved estimating the percentage of fish active and inactive within each habitat patch for each taxon (raw abundance was used). These day and night pairs (percentage of fish active and percentage of fish inactive) were used to create the ranks in the test for a given taxon over primary habitat types. A total of 398 habitat patches were analyzed for all taxa, with an average of 64 habitat patches compared for each taxon.

We also used nonmetric multidimensional scaling (NMS) to examine associations between day and night fish abundance with depth and with primary habitat (McCune and Grace, 2002). PC-ORD software, vers. 5.0 (MjM Software, Gleneden Beach, OR), was used with a Monte Carlo test and Sørensen distance measure, starting with random configurations (Mather, 1976). We restricted the NMS to taxa that showed significantly greater abundance during day or night in the Wilcoxon signed-rank test ($P<0.05$), and to those that showed a strong correlation (Pearson and Kendall correlation) with depth ($R<-0.5$ or >0.5 on the second axis) during trial NMS runs with all 31 taxa. A total of 11 taxa met these criteria. The final species (taxa) matrix included columns of log-transformed abundance and rows of sample units grouped by primary habitat for each dive during day and night (e.g., boulder-night-R534). All primary habitat types were used because the NMS determines correlation strength along an environmental gradient and does not require paired plots as in the Wilcoxon signed-rank test. The final environmental matrix included two quantitative variable columns: primary habitat types (flat rock, rock ridge, boulder, cobble, pebble, sand, and mud) and average depth (meters). Sample units greater than 3.0 standard deviations were excluded from analysis. The final ordination had 166 iterations and 15 runs. This test enabled us to determine if marked differences in fish abundance were associated with depth and primary habitat, and whether taxa showing significantly greater abundance during day or night were distributed similarly on the bank.

Results

A total of 29,787 individual fish were counted on the ROV transect videotapes. During the day, we observed an average of 207 fishes per hectare, and at night we observed a lower average of 141 fishes per hectare. Fish taxa in greatest abundance were from the genus *Sebastes*. Dominant taxa (pygmy and Puget Sound rockfish, and unidentified juvenile rockfish) showed the largest differences in relative abundance between day and night (Fig. 3). Across all stations and primary habitat types, and within at least one primary habitat type, eight taxa showed significantly greater abundance during the day ($P<0.05$) and five taxa exhibited significantly greater abundance during the night ($P<0.05$, Table 1 , Fig. 3). Three taxa were found to be significantly greater in abundance during day (kelp greenling and unidentified mottled poacher [Agonidae]) and night (redstripe rockfish [*S. proriger*]) only in specific primary habitat types (Table 1). Several taxa showed apparent differences in abundance, but sample sizes were too small for statistical significance in the paired Wilcoxon signed rank test (e.g., kelp greenling). Harlequin rockfish (*S. variegatus*) was the only species we regularly encountered exclusively at night (darkblotched rockfish were rare but were also seen only at night), whereas kelp greenling were encountered only during the day at shallow depths.

NMS analysis of distribution

The NMS analysis showed significant correlations ($P=0.03$) among taxa, depth, primary habitat, and day and night (Fig. 4). The ordination explained 78% of the variation with an acceptable stress value (a lower value

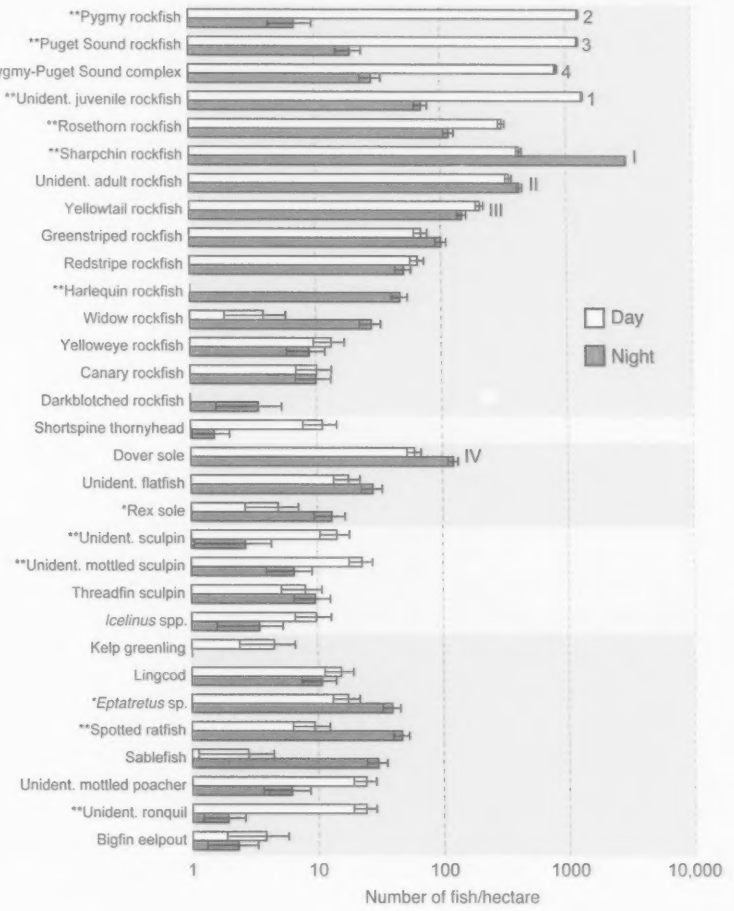

Figure 3

Total abundance (number of fish per hectare) of fish taxa as determined from the ROV during night and daytime transects over all habitat types. Wilcoxon signed-rank test was used to compare day and night abundance across stations and primary habitat types (*$P<0.05$, **$P<0.01$). Arabic numerals indicate the most dominant taxa during day, and Roman numerals indicate the most dominant taxa during night. Error bars indicate standard error of the abundance for each taxon. White bars represent day abundance and gray bars represent night abundance for the following species groups: *Sebastes*, *Sebastolobus*, flatfishes, Cottidae, and other fish. Scientific names for all taxa include from top to bottom: pygmy rockfish (*S. wilsoni*), Puget Sound rockfish (*S. emphaeus*), unidentified juvenile rockfish less than 10 cm long (*Sebastes* spp.), rosethorn rockfish (*S. helvomaculatus*), sharpchin rockfish (*S. zacentrus*), unidentified adult rockfish (*Sebastes* spp.), yellowtail rockfish (*S. flavidus*), greenstriped rockfish (*S. elongatus*), redstripe rockfish (*S. proriger*), harlequin rockfish (*S. variegatus*), widow rockfish (*S. entomelas*), yelloweye rockfish (*S. ruberrimus*), canary rockfish (*S. pinniger*), darkblotched rockfish (*S. crameri*), shortspine thornyhead (*S. alascanus*), Dover sole (*Microstomus pacificus*), unidentified flatfish (Pleuronectidae), rex sole (*Glyptocephalus zachirus*), unidentified sculpin (Cottidae), unidentified mottled sculpin (Cottidae), threadfin sculpin (*Icelinus filamentosus*), *Icelinus* spp., kelp greenling (*Hexagrammos decagrammus*), lingcod (*Ophiodon elongatus*), unidentified hagfishes (*Eptatretus* spp.), spotted ratfish (*Hydrolagus colliei*), sablefish (*Anoplopoma fimbria*), unidentified mottled poacher (Agonidae), unidentified ronquil (Bathymasteridae), and bigfin eelpout (*Lycodes cortezianus*). Alternate shading of the background represents general taxonomic groups.

Table 1

Fish taxa exhibiting significantly greater relative abundance (number of fish per hectare) across all stations over primary habitat types at Heceta Bank, OR, (rock ridge, boulder, cobble, and mud) during daytime or nighttime. Wilcoxon signed-rank test was used (*P<0.05, **P<0.01) to compare day and night relative abundance between habitat patches in closest geographic proximity within primary habitat types over all stations. Taxa are listed in order of relative abundance from top to bottom; primary habitat is listed in decreasing order of size from left to right, and numbers in parentheses are relative abundance during day or night.

Taxon	Rock ridge	Boulder	Cobble	Mud
Significantly more abundant during day				
unidentified juvenile rockfish (*Sebastes* spp.)	(1498)**	(2123)*	(632)**	(150)*
Puget Sound rockfish (*S. emphaeus*)			(2235)**	(421)**
pygmy rockfish (*S. wilsoni*)	(4878)**	(46)*	(634)**	
pygmy-Puget Sound complex (*S. wilsoni* and *S. emphaeus*)	(3240)*			
rosethorn rockfish (*S. helvomaculatus*)	(249)**		(291)*	(124)*
unidentified ronquil (Bathymasteridae)	(16)**			(43)*
unidentified mottled sculpin (Cottidae)			(30)**	
unidentified sculpin (Cottidae)			(12)*	(28)**
unidentified mottled poacher (Agonidae)			(12)*	
kelp greenling (*Hexagrammos decagrammus*)		(6)*		
Significantly more abundant during night				
sharpchin rockfish (*S. zacentrus*)	(460)**	(1134)*	(5603)*	(1656)*
redstripe rockfish (*S. proriger*)	(90)*			
harlequin rockfish (*S. variegatus*)			(103)**	
spotted ratfish (*Hydrolagus colliei*)			(75)*	(56)*
unidentified hagfishes (*Eptatretus* spp.)			(45)*	(64)*
rex sole (*Glyptocephalus zachirus*)				(69)*

denotes a better "fit" of data) of 20.5 for three axes. After a +115° rotation, the first axis showed correlation with day (right side) and night (left side) sample units, explaining 22% of the variation in the data and revealed a mean stress of 49.8. The second axis explained an additional 30% of the variation in the data and showed a negative correlation with depth (Pearson's r=0.141) and a mean stress of 29.1. The second axis also showed a positive correlation with substrate, and larger-size primary habitat was found in the first and second quadrants of the graph and smaller-size primary habitat in the third and fourth quadrant. The third axis improved the cumulative coefficient of determination, r^2, to 0.777 with little additional stress; this axis enabled us to rotate the ordination in three dimensions to distinguish habitat and species and showed good correlations with the day-night and habitat-depth axes, but is not easily plotted. Higher dimensions showed little improvement in model fit.

Taxa more abundant during the day (rosethorn rockfish, pygmy rockfish, pygmy-Puget Sound rockfish complex, kelp greenling, and unidentified juvenile rockfish) showed a positive correlation along axes one and two and appear in the upper right quadrant of Figure 4. Puget Sound rockfish showed a correlation with the day-night axis, but this species was associated with greater depth and smaller-size substrate as primary habitat when compared to the other taxa that were more abundant during the day; this taxon appears in the lower right quadrant. Thus, this dominant day assemblage was observed mainly at shallow- to mid-depths over medium to large-size substrata. Taxa showing greater abundance during the night (spotted ratfish [*Hydrolagus colliei*], hagfishes, rex sole [*Glyptocephalus zachirus*], sharpchin rockfish [*S. zacentrus*], and harlequin rockfish) showed a negative correlation along axes one and two. Thus, the dominant night assemblage was generally over deeper areas of medium- to small-size substrata of cobble and mud.

Day and night species assemblages

During the day within all stations, large densities of mostly small-size rockfish taxa were primarily found over shallow rock ridge, boulder, and cobble substrata (Table 1, Figs. 3 and 4). The four most dominant day taxa (both active and inactive) were pygmy rockfish, Puget Sound rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish. Yellowtail rockfish (*S. flavidus*) were also an important component of the daytime assemblage, albeit less abundant and less dominant during night. Many of these taxa showed significantly greater abundance and activity over medium- to large-size habitat (cobble, boulder, and rock ridge) (Tables 1 and 2). Rosethorn rockfish showed the clearest diurnal pattern of all species (Table 2). Small rockfishes and yellowtail rockfish were more active during the day but did not exhibit clear inactivity during the night.

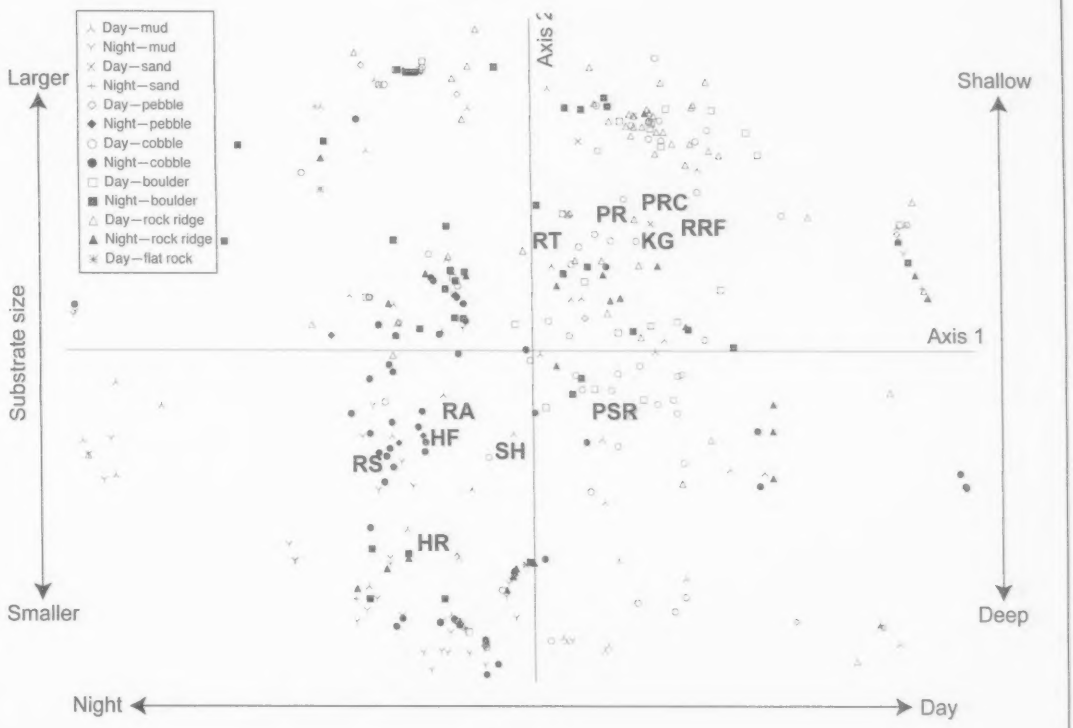

Figure 4

Nonmetric multidimensional scaling (NMS) ordination showing association between 11 taxa and habitat patches (different symbols) from all stations (2, 3, 4, 6, and 9). Taxa codes are: HF (hagfishes, *Eptatretus* spp.), HR (harlequin rockfish, *S. variegatus*), KG (kelp greenling, *Hexagrammos decagrammus*), PR (pygmy rockfish, *S. wilsoni*), PRC (pygmy-Puget Sound complex, *S. wilsoni* and *S. emphaeus*), PSR (Puget Sound rockfish, *S. emphaeus*), RA (spotted ratfish, *Hydrolagus colliei*), RS (rex sole, *Glyptocephalus zachirus*), RT (rosethorn rockfish, *S. helvomaculatus*), RRF (unidentified juvenile rockfish, *Sebastes* spp.), and SH (sharpchin rockfish, *S. zacentrus*). Environmental variables include the quantitative variable of depth (increasing depth from top to bottom), and the categorical variables (shape of symbols) of day, night, and habitat.

When compared to the dominant day assemblage, the night assemblage exhibited lower overall densities and consisted of less active, larger-size fish of fewer taxa, many of which were also seen during the daylight hours (Tables 1 and 2, Fig. 3). Dominant night taxa were sharpchin rockfish, yellowtail rockfish, Dover sole (*Microstomus pacificus*), and greenstriped rockfish (*S. elongatus*). Of the dominant night assemblage, sharpchin rockfish comprised over half of the fish encountered at night (Fig. 3) and was one of the only taxa that showed significantly greater abundance during the night ($P<0.05$) in most primary habitat types (Table 1). Hagfishes and spotted ratfish were significantly greater in abundance and activity during the night ($P<0.05$), and widow rockfish showed significantly greater activity during the night ($P<0.05$), despite being rarely observed (Table 2). Hagfishes were the only taxa that exhibited a distinct nocturnal activity pattern ($P<0.05$).

Discussion

The relative composition of fish taxa over all depths and habitat types on Heceta Bank did not show a broad replacement from day to night, as observed in shallow tropical areas. However, there were consistent patterns of abundance and activity that were species-, depth-, and habitat-specific. There was a considerable day-night change in the abundance of the four most dominant day taxa (pygmy rockfish, Puget Sound rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish) over shallower areas of rock ridge and boulder habitat. Active, small- to medium-size fish taxa tended to aggregate around shallow medium- to large-size habitat features during the day, and larger-size night taxa (sharpchin rockfish, yellowtail rockfish, Dover sole, and greenstriped rockfish) tended to aggregate around these features at night. Rosethorn rockfish

Table 2

Fish taxa (raw counts) exhibiting a significant difference in the percentage of fish found to be active and inactive during day and night within similar primary habitat types (rock ridge, boulder, cobble, and mud) over all stations at Heceta Bank, OR. Values represent the percentage of fish found to be active or inactive over each substrate type, and values in parentheses indicate *n* for each comparison. Wilcoxon signed-rank test was used (*P<0.05, **P<0.01, not significant [ns], P>0.05). Taxa are listed in order of highest abundance (number of fish per hectare) within each category.

Taxon	Primary habitat	Day active fish	Day inactive fish	Night active fish	Night inactive fish
Diurnal					
rosethorn rockfish (*S. helvomaculatus*)	rock ridge	76% (246)**			ns
	boulder	74% (243)**			85% (123)**
	cobble	66% (405)*			92% (143)**
	mud	ns			93% (47)**
Nocturnal					
Eptatretus spp.	cobble		87% (23)*	69% (29)*	
Significantly more active during day					
unidentified juvenile rockfish	rock ridge	99% (855)**			
(*Sebastes* spp.)	boulder	98% (1214)**			
	cobble	96% (876)**			
	mud	91% (54)**			
Puget Sound rockfish (*S. emphaeus*)	boulder	71% (367)**			
	cobble	73% (2501)**			
	mud	87% (126)**			
pygmy rockfish (*S. wilsoni*)	rock ridge	99% (855)**			
	cobble	99% (235)**			
	mud	94% (34)**			
yellowtail rockfish (*S. flavidus*)	rock ridge	95% (259)**			
	boulder	96% (260)**			
Significantly more active during night					
spotted ratfish (*Hydrolagus colliei*)	boulder			87% (16)*	
	mud			92% (87)*	
widow rockfish (*S. entomelas*)	boulder	96% (45)*			

and hagfishes exhibited distinct diurnal and nocturnal activity, respectively. These day and night patterns were similar to those observed during day-time surveys from manned submersibles on Heceta bank (Pearcy et al., 1989; Stein et al., 1992; Hixon et al.[2]), day and night surveys on Stonewall Bank (Hixon and Tissot[1]), and are generally consistent with most patterns found in other shallow temperate day and night studies, but were much less distinct than those for fishes inhabiting tropical fish communities (Helfman, 1978). The overall marked decrease in abundance and activity of smaller-size taxa at night was similar to the decrease that Ebeling and Bray (1976) and Moulton (1977) observed, but our study did not provide evidence of a pronounced replacement of diurnally active taxa by exclusively nocturnal species as observed at Santa Catalina Island (Hobson and Chess, 1973; Hobson et al., 1981), Hawaiian tropical reefs (Hobson, 1972), and reefs in the Virgin Islands (Colette and Talbot, 1972).

It is possible that light illumination at the top of Heceta Bank during the day contributed to the higher abundance and activity of the three most dominant day taxa (pygmy rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish), as found in similar studies on temperate species. Fishes found at the top of Heceta Bank likely perceive and use the faint sun illumination during the day (Boehlert, 1979). On Heceta Bank, the photic zone generally extends down to approximately 50 m water depth and it is generally accepted that sun illumination affects behavior of fishes down to these depths (L. Britt, personal commun.[4]). This was confirmed by the GLOBEC survey, which measured one percent of surface light at 50 m, just above the shallowest fish survey depths (70 m) where most of the unidentified juvenile rockfish were present. Light illumination may be aiding the dominant day assemblage because these taxa stay close (perhaps within visual distance) to large features that provide refuge from larger, active piscivorous predators. In Puget Sound

[4] Britt, Lyle L. 2007. Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way N.E., Seattle, WA 98115.

(Moulton, 1977), on rocky kelp forests off Santa Barbara, California (Ebeling and Bray, 1976), and on Santa Catalina Island, California (Hobson and Chess, 1976; Hobson et al., 1981), the small-size adult and juvenile rockfish that remain exposed from refuge during the night stay close to the seafloor.

Only two taxa showed distinct day and night activity patterns (diurnal: rosethorn rockfish and nocturnal: hagfish), indicating that marked differences in day and night activity are not as prevalent as those found in shallow tropical coral reef and temperate fish communities (Table 2) (Hobson, 1972; Helfman, 1978). The diurnal activity pattern exhibited by rosethorn rockfish was independent of habitat, indicating that habitat type may not be a significant factor in determining differences between day and night activities for this species (Tables 1 and 2). The nocturnal activity pattern that hagfishes exhibited was similar to that observed by Ooka-Souda et al. (1985) of another hagfish species (*Eptatretus burgeri*), in the laboratory. During the day on Heceta Bank, most hagfish were observed coiled up over mud or sand, or around cobble, whereas during the night fish of this taxon was observed swimming above bottom or moving in contact with the bottom in a twisted manner. Like silver hake (*Merluccius bilinearis*) which use sand waves (transverse ridges of sand) for refuge during the day (Auster et al., 2003) and that forage during the night (Bowman and Bowman, 1980; Auster et al., 1995), hagfishes on Heceta Bank may use mid-depth cobble and mud habitats for resting during the day and may forage at night. Not all rosethorn rockfish and hagfishes strictly followed a diurnal or nocturnal activity pattern; however, the fish activity measure we used was not sensitive enough to detect subtle differences in behavior, such as resting individuals found hovering close to but not in contact with the seafloor.

Potential bias exists in observing and attempting to quantify activity in fishes when using video survey methods (Uzmann et al., 1977; Sale and Douglas, 1981; Wakefield and Smith, 1990). Our inability to identify many of the rockfishes to species is potentially problematic, and illustrates a limitation of this survey method. The majority of historical studies show that very few fishes exhibit changes in activity with the presence of an ROV or submersible, although a handful of taxa do show behavioral responses (High, 1980; Carlson and Straty, 1981; Pearcy et al., 1989). SCUBA-based video surveys of fish abundance and behavior indicate that although the majority of fishes show no noticeable reaction, some species may avoid or be attracted to divers outside the camera's field of visibility and may even follow divers (Moulton, 1977). It has been argued that SCUBA surveys do not significantly affect counts because most fishes that follow divers remain behind the field of view of the camera (Powles and Barans, 1980). In our study, anecdotal evidence indicated that the ROV had limited effect on fish behavior, except in cases where the ROV came in contact with the substrata. Further investigation is needed, however, to fully grasp the impacts of observational vehicles on fish responses (Stoner et al., 2008).

Implications for groundfish surveys

Day and night activity patterns in demersal fishes have been shown to dramatically change the catchability of some species on the West Coast (Hannah et al., 2005), in the Northwest Atlantic (Bowman and Bowman, 1980), in Newfoundland (Casey and Myers, 1998), and in the North Sea (Petrakis et al., 2001). In this study, we found that daytime surveys could underestimate the abundance of certain species that are more abundant or active at night, such as sharpchin rockfish. Highly significant differences in day and night abundance of schooling rockfishes found in this study indicate that daytime trawl surveys over small- to medium-size habitat features may be biased for some fish species. Migration of fishes into the overlying water column, horizontally off the bank, or into hiding among medium- to large-size features is likely the most common day and night behaviors that would decrease the availability of fishes to the ROV. Specifically, Puget Sound rockfish may be more available over deeper, smaller-size rock structures, whereas other dominant day taxa (pygmy rockfish, pygmy-Puget Sound rockfish complex, and unidentified juvenile rockfish) and sharpchin rockfish are likely less available to trawl surveys over large-size features in shallower portions of the bank. We speculate that the reduction in abundance of the four most dominant day taxa is due to fish seeking refuge around medium- to larger-size structures because of the potential presence of large piscivores (Wilkins, 1986; Adams, 1987), rather than to schooling in the water column.

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Distribution, growth, and mortality of sailfish (*Istiophorus platypterus*) larvae in the northern Gulf of Mexico

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Abstract—Ichthyoplankton surveys were conducted in shelf and slope waters of the northern Gulf of Mexico during the months of May–September in 2005 and 2006 to investigate the potential role of this region as spawning and nursery habitat of sailfish (*Istiophorus platypterus*). During the two-year study, 2426 sailfish larvae were collected, ranging in size from 2.0 to 24.3 mm standard length. Mean density for all neuston net collections (n=288) combined was 1.5 sailfish per 1000 m^2, and maximum density was observed within frontal features created by hydrodynamic convergence (2.3 sailfish per 1000 m^2). Sagittal otoliths were extracted from 1330 larvae, and otolith microstructure analysis indicated that the sailfish ranged in age from 4 to 24 days after hatching (mean=10.5 d, standard deviation [SD]=3.2 d). Instantaneous growth coefficients (g) among survey periods (n=5) ranged from 0.113 to 0.127, and growth peaked during July 2005 collections when density within frontal features was highest. Daily instantaneous mortality rates (Z) ranged from 0.228 to 0.381, and Z was indexed to instantaneous weight-specific growth (G) to assess stage-specific production potential of larval cohorts. Ratios of G to Z were greater than 1.0 for all but one cohort examined, indicating that cohorts were gaining biomass during the majority of months investigated. Stage-specific production potential, in combination with catch rates and densities of larvae, indicates that the Gulf of Mexico likely represents important spawning and nursery habitat for sailfish.

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Declining populations of Atlantic sailfish (*Istiophorus platypterus*) (ICCAT, 2001) emphasize the need for a better understanding of their biology, especially processes affecting growth and mortality during early life because these mechanisms often regulate recruitment (Fuiman, 2002). To date, studies on sailfish biology during the early life interval are limited; however, recent research conducted in the Straits of Florida indicates that sailfish grow rapidly and experience high mortality during early life (Luthy et al., 2005; Richardson et al., 2009a). Although our understanding of the early life ecology of sailfish has improved in recent years, work to date has been limited in geographic scope and basic life history data on sailfish are limited or not available for other regions of the Atlantic that may represent essential spawning and nursery habitat of sailfish. In particular, bycatch data from pelagic longline fisheries in the Gulf of Mexico indicate that catch rates for sailfish are twofold higher in the Gulf than in other areas of the North Atlantic during the presumed spawning season (May–September; de Sylva and Breder, 1997; NMFS[1]). Because spawning stock biomass appears high in this region, a better understanding of the role of the Gulf of Mexico as spawning and early life habitat of Atlantic sailfish is essential.

The Gulf of Mexico supports one of the most productive fisheries in the world (Chesney et al., 2000), and oceanographic features within the Gulf are influenced by inflow from the Mississippi River and large-scale oceanographic features, such as the Loop Current and associated warm and cold core eddies (Govoni and Grimes, 1992; Sturges and Leben, 2000). Physicochemical conditions and primary production vary markedly within and across these features (Grimes and Finucane, 1991; Biggs, 1992), and have been shown to affect the distribution and growth of pelagic larvae in the Gulf (Govoni et al., 1989; de Vries et al., 1990; Lang et al., 1994). Namely, higher densities

[1] NMFS (National Marine Fisheries Service. 2008. NMFS Pelagic Longline Logbook data, (http://www.sefsc.noaa.gov/flslandingsdata.jsp, accessed December 2008).

and increased growth have been observed for larvae within frontal features created by riverine discharge and hydrodynamic convergence (Lang et al., 1994; Hoffmeyer et al., 2007). It is likely that oceanographic features also influence the early life ecology and population dynamics of sailfish in this region, and therefore an improved understanding of the effects of these features on distribution, growth, and survival will aid in determining the value of the Gulf as spawning and nursery habitat for sailfish.

The objectives of this research were threefold: 1) to characterize spatial and temporal patterns of abundance of sailfish larvae in the northern Gulf of Mexico; 2) to relate spatial variation in distribution and growth to oceanographic features to determine the causal factors responsible for recruitment variability; and 3) to estimate demographic parameters within and across years to determine whether these traits varied temporally. Estimates of growth (G) and mortality (Z) were combined (G:Z) to determine indices of stage-specific production potential and to assess the functional role of the Gulf as spawning and nursery habitat of this species.

Materials and methods

Field collections

Five ichthyoplankton surveys were conducted in shelf and slope waters of the northern Gulf during spring and summer of 2005 (May, July, and September) and summer of 2006 (June and August). Surveys were conducted in an area bounded by 27° to 28°N latitude and 88 to 94°W longitude. This sampling area was selected because bycatch rates of adult sailfish by U.S. longliners were high in this region during the presumed spawning period of Atlantic sailfish (NMFS[1]). Istiophorid larvae were collected with paired neuston nets (2-m width×1-m height frame) with two mesh sizes (500 µm and 1200 µm) to account for potential differences in capture success between mesh sizes. Nets were towed through the top meter of the water column at approximately 2.0 knots for 10 minutes. Paired tows were taken at 60 to 70 sampling stations spaced approximately 15 kilometers (km) apart during each survey. Sampling was conducted at 15-km intervals to allow coverage of a large area encompassing multiple oceanographic features. The September 2005 survey was shortened (39 stations sampled) because of inclement weather.

At each station, sea surface temperature (°C), salinity (ppt), and dissolved oxygen (mg/L) were recorded by using a Sonde 6920 Environmental Monitoring System (Yellow Springs Instruments Inc., Yellow Springs, OH). A probe malfunctioned during sampling in August 2006, preventing dissolved oxygen measurements. Sea surface height (cm) for each station was determined from archived satellite altimetry data provided by the Colorado Center for Astrodynamics Research (CCAR) Real-Time Altimetry Project (argo.colorado.edu; R. Leben, personal commun.[2]). Flowmeters (General Oceanics, model 2030R, Miami, FL) placed within each net were used to determine the surface area sampled by each net. A formula provided by the manufacturer was used to determine distance towed during each collection which was multiplied by net width to determine surface area sampled during each collection (m^2): *surface area sampled* (m^2) = *distance sampled* (m) × 2 m (net width).

Fish larvae and associated biota were preserved onboard in 95% ethanol and istiophorids were sorted from each sample in the laboratory with the use of a Leica MZ stereomicroscope and stored in 70% ethanol. Istiophorid larvae were photographed and standard length (SL) was measured to the nearest 0.1 mm. Istiophorids do not have a full complement of fin rays until reaching 20 mm SL (Richards, 1974), and 99.8% of specimens collected in the Gulf were less than 20 mm. Even though a small number of our largest specimens were over 20 mm and may be considered early juveniles (n=3), for the purposes of this study, all sailfish collected are referred to as larvae.

Genetic identification

A percentage of istiophorid larvae (22.2%) were identified to the species level by following the protocol of Bangma (2006). The protocol was subsequently modified and the remaining istiophorid larvae (77.8%) were identified according to the protocol of J. Magnussen and M. Shivji (personal commun.[3]). Briefly, a single eyeball was removed from each larva and DNA was extracted by using a QIAGEN DNeasy blood and tissue kit (QIAGEN #69506, Valencia, CA). A multiplex polymerase chain reaction (PCR) was performed by using an Eppendorf mastercycler gradient, QIAGEN Hot Star Taq DNA Polymerase (QIAGEN #203203), and PCR grade dNTP mix (QIAGEN #201901). Four primer pairs were used in each PCR reaction: a universal billfish primer set, and species-specific primers for sailfish, white marlin, (*Kajikia albida*), and blue marlin (*Makaira nigricans*). PCR reactions were examined by means of gel electrophoresis with 1% agarose gels containing ethidium bromide and species identification was based on gel banding patterns. This multiplex assay was employed to identify sailfish larvae as follows. For samples consisting of less than 10 individuals, all specimens were assayed. For samples with 10–50 istiophorid larvae, 40–60% of larvae were processed. For samples with >50 istiophorid larvae, 25% of larvae were processed. If all larvae in a particular subsample were identified as conspecific, remaining larvae from the sample were assigned to that species. If more than one istiophorid species was detected in a subsample, all remaining larvae from the sample were identified genetically.

[2] Leben, Robert. 2008. Colorado Center for Astrodynamics Research, Univ. Colordao, Boulder, CO.

[3] Shivji, Mahmood. 2007. Guy Harvey Research Institute, Nova Southeastern Univ., Ft. Lauderdale, FL.

Density and catch rate

The total number of sailfish caught at each sampling station was divided by the surface area sampled to determine the density of larvae in number of individuals per 1000 m^2. Mean density did not vary between the two mesh sizes (500 µm and 1200 µm) in any survey (paired t-test, all $P \geq 0.05$), indicating no difference in capture success between net sizes. However, mean standard length was smaller in the 500-µm net gear (5.2 mm vs. 5.6 mm; $F_{(1,3116)}=21.3$, $P<0.01$), indicating that a larger fraction of small larvae were retained by the finer mesh. Frequency of occurrence was calculated for each survey as the number of collection stations which produced at least one sailfish larva by using the equation

$$\textit{Frequency of occurrence} = (\textit{number of stations with} \geq 1 \textit{ larva / total number of stations during survey}) \times 100. \quad (1)$$

In order to compare catch rates with those from other ichthyoplankton studies, catch per unit of effort (CPUE) of sailfish larvae was estimated with the equation

$$\textit{CPUE} \text{ (larvae per hour)} = \textit{number of larvae collected} / ([\textit{number of tows} \times \textit{tow length} \text{ (min)} \times 2 \textit{ (number of nets towed)}] / 60). \quad (2)$$

Oceanographic features

Remotely sensed sea surface height (SSH) data were used to delineate oceanographic features into one of four categories (Leben et al., 2002). Briefly, stations with a SSH greater than 17 cm were considered to be within the core of the Loop Current or an associated eddy system and classified as "anticyclones" (warm core eddies) (Leben et al., 2002). Further, the core of adjacent "cyclones" (cold core eddies) were identified by a SSH of less than –10 cm. Frontal features associated with the Loop Current and anticyclones have been reported to extend up to 60 km from the 17-cm contour. Therefore, stations between 17 cm and –10 cm SSH and within 60 km of the 17 cm SSH contour were classified as being in a "front" (Tidwell, 2008). Remaining stations were classified as "open ocean."

Analysis of otolith microstructure

Sagittal otoliths were extracted, cleaned of tissue in immersion oil, and preserved in mounting media (Flotexx, Fisher Scientific #14-390-4, Pittsburgh, PA) for a subset of sailfish larvae. Mounted otoliths were photographed under high magnification (400×) with an Olympus BX41 light microscope, and daily growth increments were enumerated with the use of Image-Pro Plus software (vers. 4.5, Media Cybernetics Inc., Bethesda, MD) by counting the first visible increment beyond the hatch check as day one (Luthy et al. 2005). Inner increments of large otoliths are occasionally difficult to enumerate; therefore a regression of growth increment radius on age was used to predict the number of increments at various distances from the core (Rooker et al., 1999). The number of increments within unclear regions was estimated with this regression and added to the increment count for the enumerated section to produce final age estimates. Less than 25% of age estimates were corrected with this method, and if the unclear region comprised more than 33% of the final age estimate, the otolith was not used for age and growth assessments. Two independent readings of daily increments were conducted by a single reader for each otolith. When two readings were within 10% variance of each other, one reading was randomly selected for analysis. If readings differed by >10%, a third reading was performed. If the third reading was within 10% variance of one of the former readings, one of the two similar readings was randomly selected for analysis. If each reading differed from the others by >10%, the otolith was not used for further analysis (n=94, 7.1%).

Growth, mortality and hatch dates

Growth rates were determined by using otolith-derived age estimates (n=1236) and standard length data. Because ages varied among surveys, growth rates were based on a limited age range (≤17 days or the oldest larva in May 2005 collections) to minimize any effect of variable age ranges on growth analyses (Rilling and Houde, 1999). Daily instantaneous growth coefficients (g) were calculated from an exponential model:

$$L_t = L_0 e^{gt}, \quad (3)$$

where L_t = length (mm SL) at time t;
L_0 = estimated length at hatching;
g = instantaneous growth coefficient (d); and
t = otolith-derived age (days after hatching).

Ages of sailfish without an otolith-derived age were predicted by using age-length relationships (n=1118). A small number of sailfish larvae were damaged (n=72), and therefore length and age estimates could not be determined for these larvae.

Daily mortality was estimated for each survey from regressions of the decline in $\log_e$(*abundance*+1) on *age*. In order to minimize the influence of gear avoidance by larger larvae (Houde, 1987), mortality estimates were determined over a short time interval (10 days), and thus for a limited size range of larvae (<10 mm). Mortality was calculated for several time intervals ranging from 5 to 10 days and differences were negligible, indicating that the 10-day duration was appropriate for the target life stage. The age of peak abundance for each cohort was used as the initial point for catch-curve analysis and ranged from 9 to 11 days after hatching. Daily instantaneous mortality rates (Z) were calculated from the exponential model

Table 1

Mean environmental conditions (± standard deviation [SD]) by oceanographic feature for ichthyoplankton collections in the northern Gulf of Mexico in 2005 and 2006. Environmental parameters were recorded at the surface at each sampling station.

Feature	Temperature (°C)	Salinity (ppt)	Dissolved oxygen (mg/L)
Anticyclone	29.1 (1.6)	36.1 (0.4)	6.8 (0.8)
Front	28.9 (1.4)	36.1 (0.4)	6.6 (0.5)
Open ocean	29.3 (1.6)	35.5 (1.2)	6.7 (0.8)
Cyclone	28.2 (2.0)	35.6 (0.6)	7.2 (1.3)

$$N_t = N_0 e^{-Zt}, \quad (4)$$

where N_t = abundance at time t;
N_0 = estimated abundance at hatching;
Z = instantaneous mortality coefficient (d); and
t = otolith-derived age.

Dry weight (mg) was calculated for all larvae with a measured length by using the length-weight relationship for sailfish larvae by Luthy et al. (2005): *weight* (mg) = $0.002(SL[\text{mm}])^{3.012}$. Weight-at-age data were fitted with exponential growth models to determine instantaneous weight-specific growth coefficients (G) for each survey by using the equation

$$W_t = W_0 e^{Gt}, \quad (5)$$

where W_t = dry weight (mg) at time t;
W_0 = estimated weight at hatching;
G = instantaneous weight-specific growth coefficient (d); and
t = otolith-derived age.

Indices of stage-specific production potential were assessed for each cohort by examining the ratio of instantaneous weight-specific growth to daily mortality (G:Z). This ratio incorporates growth and mortality and was used as an index of stage-specific production of larval cohorts (Rilling and Houde, 1999; Rooker et al., 1999; Wells et al., 2008). A cohort with a G:Z>1.0 was considered to be gaining biomass, which indicates that individuals had increased survival and production potential (Houde and Zastrow, 1993; Wells et al., 2008).

Hatch dates for larvae were determined by subtracting age from date of collection. Otolith-derived ages were used when available, and remaining ages were predicted by applying cohort-specific age-length keys. Given that larger, older larvae in our collections hatched earlier and experienced greater cumulative mortality than larvae that hatched later, adjustments for mortality were made to more effectively represent the hatch dates of survivors in our collections by using the equation

$$N_0 = N_t \,/\, e^{-Zt}, \text{ (Powell et al., 2004)}, \quad (6)$$

where N_0 = estimated number of larvae at hatching;
N_t = number of larvae at time t (N_t=1 because N_0 was calculated for each individual larva);
Z = cohort-specific daily instantaneous mortality rate; and
t = age of larva in days.

Data analysis

Spatial and temporal variation in environmental conditions and density of sailfish larvae was examined with a two-way analysis of variance (ANOVA) (factors: oceanographic feature and survey). Because of uneven replicates in 2005 and 2006, separate one-way ANOVAs were conducted to assess inter- and intra-annual variation in length and age of sailfish with year or survey as a fixed factor. In order to minimize heteroscedasticity, estimates of density were $\log_e$+1 transformed, whereas standard length and age data were $\log_e$ transformed. In cases where variances were unequal, nonparametric analyses (Brown-Forsythe F-Test; Brown and Forsythe, 1974) were performed; however, results were consistent with parametric tests (ANOVA) and thus only parametric analyses are presented. *Post-hoc* differences among levels of the main effect(s) were examined with Tukey's honestly significant difference (HSD) test when variances were equal and with a Dunnett's T3 test when variances were unequal (Zar, 1996). Analysis of covariance (ANCOVA) was used to test for spatial and temporal variations in growth and mortality (covariate: age) with models to determine if the slopes of the regression lines differed (slopes test). All data analyses were performed with SPSS, vers. 15.0 (SPSS Inc., Chicago, IL) with α=0.05.

Results

Environmental conditions

Spatial and temporal variations in environmental conditions were observed during Gulf collections. Temperatures were not significantly different among oceanographic features (ANOVA, $F_{(3,270)}$=2.2, P=0.09), albeit temperature was lowest within cyclones (28.2°C) compared with other oceanographic features (28.9–29.3°C) (Table 1). Mean temperature was 28.8°C and 29.4°C in 2005 and 2006, respectively, and varied significantly among the five surveys (ANOVA, $F_{(4,270)}$=354.0,

Table 2

Mean environmental conditions (± standard deviation [SD]) for ichthyoplankton surveys in the northern Gulf of Mexico in 2005 and 2006. Environmental parameters were recorded at the surface for each sampling station. Dissolved oxygen is not reported for the August 2006 survey because of a probe malfunction (NA).

Year	Survey	Date	Temperature (°C)	Salinity (ppt)	Dissolved oxygen (mg/L)
2005	May	17–22	26.4 (0.9)	35.5 (0.7)	7.1 (0.7)
	July	23–28	30.4 (0.7)	35.2 (1.3)	6.8 (1.2)
	September	16–19	29.8 (0.6)	36.5 (0.6)	6.3 (0.4)
	All surveys		28.8 (2.0)	35.6 (1.1)	6.8 (1.0)
2006	June	15–20	28.7 (0.5)	35.8 (0.4)	6.6 (0.1)
	August	31 July– 5 Aug	30.1 (0.3)	36.2 (0.4)	NA
	All surveys		29.4 (0.8)	36.0 (0.5)	NA

Table 3

Total catch, frequency of occurrence, and density (± standard deviation [SD]) of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006 arranged by survey. Number of stations during each survey (n) shown. Percent frequency of occurrence was based on collection stations during each survey that yielded 1 or more larvae.

Survey	n	Sailfish catch	Frequency of occurrence	Density (± SD) (no./1000m^2)	Maximum density	Larvae/hour
May 2005	60	212	26.7	0.6 (1.8)	10.5	10.6
July 2005	62	755	56.5	2.1 (7.5)	51.4	36.5
Sept 2005	39	134	46.2	0.6 (1.3)	4.5	10.3
June 2006	62	691	48.4	2.0 (4.7)	22.1	33.4
Aug 2006	65	634	47.0	1.7 (3.0)	10.2	25.4
Total	288	2426	45.0	1.5 (4.5)		24.4

$P<0.01$) (Table 2). Spatial variation in salinity was detected among oceanographic features (ANOVA, $F_{(3, 270)}=16.8$, $P<0.01$), and lowest salinity observed within open ocean and cyclonic features (35.5 ppt and 35.6 ppt, respectively) and higher salinity in anticyclonic and frontal features (36.1 ppt and 36.1 ppt, respectively) (Table 1). Mean salinity was 35.6 ppt and 36.0 ppt in 2005 and 2006, respectively, and significant variation was observed among the five surveys (ANOVA, $F_{(4, 270)}=11.1$, $P<0.01$) (Table 2). Dissolved oxygen (DO) varied significantly among oceanographic features (ANOVA, $F_{(3, 270)}=2.7$, $P=0.048$) and surveys (ANOVA, $F_{(4, 270)}=38.9$, $P<0.01$) (Table 2). Lower DO levels were observed within anticyclones, fronts, and the open ocean (6.8 mg/L, 6.6 mg/L, and 6.7 mg/L, respectively) compared to those within cyclonic features (7.2 mg/L) (Table 1).

Spatial and temporal patterns of abundance

A significant interaction effect between oceanographic feature and survey on the density of sailfish was detected (ANOVA, $F_{(10, 271)}=2.1$, $P=0.02$), and highest densities were observed within frontal features in three of five surveys and in the open ocean during the remaining surveys (Fig. 1). No individual effect of oceanographic feature or survey on density was observed (feature $P=0.06$, survey $P=0.11$), although density was lowest within cyclones during all surveys. When data from all surveys were combined, significant spatial variation in the density of sailfish among oceanographic features was observed (ANOVA, $F_{(3, 285)}=3.3$, $P=0.02$); density within cyclones was lower than that within other features ($P<0.05$).

Frequency of occurrence and relative abundances were highest in June (48.4%), July (56.5%), and August (47.0%) surveys and lowest during the May 2005 survey (26.7%) (Table 3). The overall density of sailfish was 1.5 larvae per 1000 m^2; lowest densities were observed in May and September 2005 surveys (0.6 larvae per 1000 m^2 and 0.6 larvae per 1000 m^2, respectively) and higher densities during July 2005 (2.1 larvae per 1000 m^2), June 2006 (2.0 larvae per 1000 m^2), and August 2006 (1.7 larvae per 1000 m^2) (Table 3). Catches peaked in July 2005 and June 2006 when maximum densities of 51.4 larvae per 1000 m^2 and 22.1 larvae per 1000 m^2 were observed, respectively (Table 3). The overall catch per unit of effort (CPUE) for sailfish in the northern Gulf was 24.4 larvae per hour, and highest CPUEs were reported for July 2005 (36.5), June 2006 (33.4), and August 2006 (25.4) (Table 3).

Table 4

Exponential growth models arranged by survey and oceanographic feature for sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Number of larvae collected within each feature is given (n). Cyclones excluded from analysis because of low sample sizes within this type of feature. * indicates significant growth difference among features.

Survey	Feature	n	Growth model
July 2005	Anticyclone	135	$1.289e^{0.128(age)}$
	Front	45	$1.458e^{0.122(age)}$
	Open ocean	108	$1.331e^{0.124(age)}$
June 2006	Anticyclone	21	$1.713e^{0.101(age)}$
	Front	108	$1.415e^{0.120(age)}$
	Open ocean	118	$1.526e^{0.112(age)}$
August 2006	Anticyclone	131	$1.682e^{0.105(age)}$*
	Front	166	$1.480e^{0.114(age)}$
	Open ocean	149	$1.442e^{0.117(age)}$*

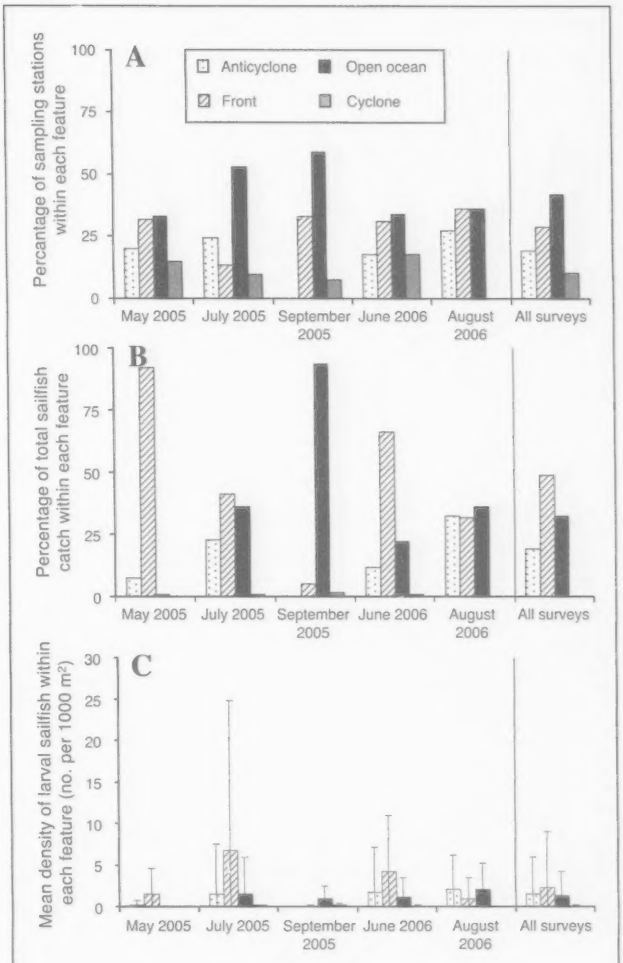

Figure 1

(**A**) Percentage of sample collections of sailfish (*Istiophorus platypterus*) conducted within each oceanographic feature during ichthyoplankton surveys the northern Gulf of Mexico in 2005 and 2006. (**B**) Percentage of sailfish larvae collected within each oceanographic feature. (**C**) Mean density of sailfish larvae within each feature. Error bars represent one standard deviation (SD).

Sailfish length and age distributions

No significant difference in mean standard lengths of sailfish was observed between 2005 (5.1 mm, standard deviation [SD]=2.1) and 2006 (4.9 mm, SD=2.0) (ANOVA, $F_{(1, 2352)}$=3.3, P=0.07) (Fig. 2). Sailfish were most abundant in the 3–6 mm size range, with 70.4% and 65.9% of the catch in this size range in 2005 and 2006, respectively. Intra-annual differences in mean lengths of sailfish were observed in 2005 (ANOVA, $F_{(2, 1034)}$=62.6, P<0.01) and 2006 (ANOVA, $F_{(1, 1315)}$=75.8, P<0.01); smallest mean lengths were observed in May 2005 (4.1 mm, SD=1.6) and June 2006 (4.5 mm, SD=1.6), and larger larvae were collected in July 2005 (5.4 mm, SD=2.2) and August 2006 (5.4 mm, SD=2.3).

Mean ages were statistically similar between 2005 (10.1 days, SD=3.1 days) and 2006 (10.5 days, SD=3.2) (ANOVA, $F_{(1, 1234)}$=2.7, P=0.10) (Fig. 2). Sailfish larvae were most abundant in the 7–11 day range, with 60.7% and 53.9% of the catch in this age range in 2005 and 2006, respectively. Significant intra-annual variation in sailfish mean ages was observed in 2005 (ANOVA, $F_{(2, 521)}$=51.6, P<0.01) and 2006 (ANOVA, $F_{(1, 710)}$=47.9, P<0.01), when youngest mean age was observed in May 2005 (8.0 days, SD=2.3) and June 2006 (9.4 days, SD=3.1), and older larvae were observed in July 2005 (11.0 days, SD=3.3) and August 2006 (11.0 days, SD=3.1).

Spatial and temporal patterns of growth

Spatial variation in growth was analyzed across oceanographic features (anticyclone, front, and open ocean) for three of the five surveys, and significant differences in growth were observed during August 2006 collections (Table 4). Cyclones were excluded from our analysis because of low sample sizes within this type of feature. During the August 2006 survey, daily instantaneous growth rates (g) of larvae collected within anticyclones (g=0.105) was significantly slower than growth of larvae collected in the open ocean (g=0.117) (ANCOVA, slopes, $F_{(2, 440)}$=3.4, P=0.03) (Table 4). In contrast, growth did not differ significantly among the three features in July 2005 (anticyclones g=0.128, fronts g=0.122, and open ocean g=0.124) and June 2006 (anticyclones g=0.101, fronts g=0.120, and open ocean g=0.112) (ANCOVA,

slopes, $F_{(2, 282)}$=0.4, P=0.67 and ANCOVA, slopes, $F_{(2, 241)}$=2.5, P=0.09, respectively).

Interannual differences in daily instantaneous growth rates of sailfish were detected between 2005 (g=0.123) and 2006 (g=0.114) (ANCOVA, slopes, $F_{(1, 1205)}$=21.4, P<0.01) (Fig. 3). Further, significant intra-annual variation in growth was observed in 2005 (ANCOVA, slopes, $F_{(2, 507)}$=5.1, P=0.01); larvae collected in September (g=0.113) displayed slower growth than larvae collected in July (g=0.127) (Fig. 4). In contrast, growth was statistically similar between surveys in 2006 (ANCOVA, slopes, $F_{(1, 692)}$=0.7, P=0.39).

Temporal variation in mortality

Estimates of daily instantaneous mortality (Z) did not differ significantly between 2005 (Z=0.288) and 2006 (Z=0.394) (ANCOVA, slopes, $F_{(1, 46)}$=1.0, P=0.33) (Fig. 5, Table 5). Mortality rates ranged from 0.228 to 0.345 among survey periods in 2005, but rates were statistically similar (ANCOVA, slopes, $F_{(2, 24)}$=2.1, P=0.15) (Fig. 6). Further, mortality rates were not significantly different between survey periods in 2006, ranging from 0.344 in June to 0.381 in August (ANCOVA, slopes, $F_{(1, 16)}$=0.5, P=0.48).

Production potential (G:Z)

Instantaneous weight-specific growth coefficients (G) were 0.371 in 2005 and 0.347 in 2006, and G was indexed to daily instantaneous mortality (Z) to assess stage-specific production potential, G:Z (Table 5). Annual estimates of G:Z were 1.29 in 2005 and 0.88 in 2006. Production potential was highest in May 2005 (1.30) and July 2005 (1.66). In contrast, G:Z ratios of the September 2005 (1.01), June 2006 (1.02), and August 2006 (0.91) surveys were lower.

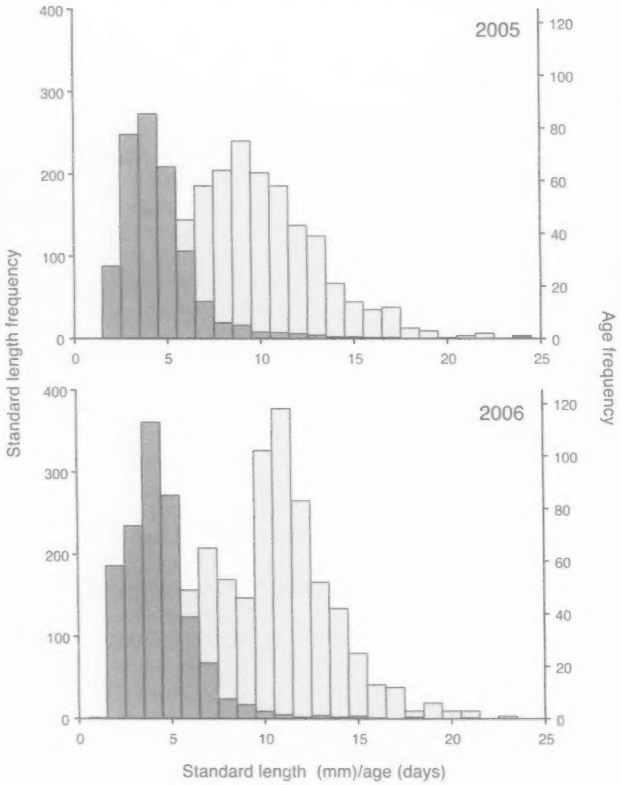

Figure 2

Standard length and age-frequency distributions of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Standard length distributions are shown in dark bars (n=1037 and n=1317 in 2005 and 2006, respectively). Age distributions are shown in light bars (n=524 and n=712 in 2005 and 2006, respectively). Note: 72 larvae indicated in Table 2 were damaged and no length measurements were taken for these larvae.

Hatch-date distribution

Age-based estimates of hatch date indicated that sailfish in our collections were spawned from May to September (Fig. 7). Hatching of sailfish peaked in mid-July, and the majority of larvae hatched in July: 56.1% according to back-calculated estimates, 73.4% according to mortality adjusted estimates. The percentage of total catch from July for mortality-adjusted hatch dates was 52.1% in 2005, and 77.1% in 2006. Because the majority of sailfish were <20 days of age and sampling was conducted bimonthly, hatch-date distributions comprised multiple cohorts from separate spawning events throughout the spawning season.

Discussion

The relative abundance of sailfish larvae collected in the present study was comparable to or higher than values reported from other putative spawning grounds of sailfish. Llopiz and Cowen (2008), collected 7.3 sailfish larvae per hour in neuston tows over a two-year period in waters of the Straits of Florida; their catch rate was lower than the catch rate of 27.4 sailfish larvae per hour reported by Post et al. (1997) in the same region. Further, Richardson et al. (2009b), during a single week, reported a catch rate of 298 sailfish larvae per hour in the Straits of Florida; this catch rate indicates that very high, but ephemeral, abundances occur in this region. Catch rates of istiophorid billfishes (sailfish, white marlin, and blue marlin) reported in other areas,

including the Bahamas (Serafy et al., 2003) and the Dominican Republic (Prince et al., 2005), were less than 10 istiophorid larvae per hour, which is markedly lower than rates reported in our study for the Gulf of Mexico (24.4 sailfish larvae per hour). Sailfish frequency of occurrence from the Gulf (45.0%) also corresponds closely to the 41.1% occurrence reported in the Straits of Florida and Bahamas by Luthy (2004), which included all Atlantic billfishes. Although CPUE was standardized for tow length, sampling gear, and number of tows, variations in towing methods as well as in the timing of sampling may have affected differences in catch rates of larvae. However, the relatively high catch rate of sailfish larvae reported in our study supports the premise that this region is an important spawning and nursery ground of sailfish—a contention supported by high bycatch rates of adult sailfish during summer months (NMFS[1]).

The highest density of larvae was reported within mesoscale frontal features and highest catch rates were observed from June through August. Lowest densities of sailfish larvae were observed in cold core features during all surveys; however, as with other pelagic species (Richards et al., 1993, Hoffmeyer et al., 2007), catches were higher within fronts and anticyclones associated with the western margin of the Loop Current. In fact, highest densities were observed within frontal features during three of five surveys and over the course of all surveys combined. Higher catches of marine fish larvae have been reported at frontal features created by riverine discharge or converging oceanic currents in both temperate and tropical oceans (Hoffmeyer et al., 2007; Richardson et al., 2009b). The accumulation of larvae near or within fronts may simply be due to hydrodynamic convergence which has been shown to aggregate marine larvae in the Gulf and other regions (Govoni and Grimes, 1992; Bakun, 2006). Alternatively, elevated primary and secondary production within frontal features often increases the availability of planktonic prey (Govoni et al., 1989; Grimes and Finucane, 1991) and therefore may effect higher survival for larvae within these oceanographic features (Grimes and Finucane, 1991; Biggs, 1992). In a recent study in the Straits of Florida, larval sailfish density was observed to peak at eddy frontal zones where there was a corresponding increase in density of common sailfish prey items (Llopiz and Cowen, 2008; Richardson et al., 2009b). This finding supports the premise that larvae are more abundant at fronts because of the increased availability of prey. As with spatial trends in sailfish density, temporal patterns in Gulf collections were comparable to those in the Straits of Florida; sailfish larvae were more abundant during spring and summer months (Post et al., 1997; Luthy, 2004). Elevated catches of sailfish in the summer correspond to peak spawning activity of sailfish in the North Atlantic (de Sylva and Breder, 1997; Richardson, 2007).

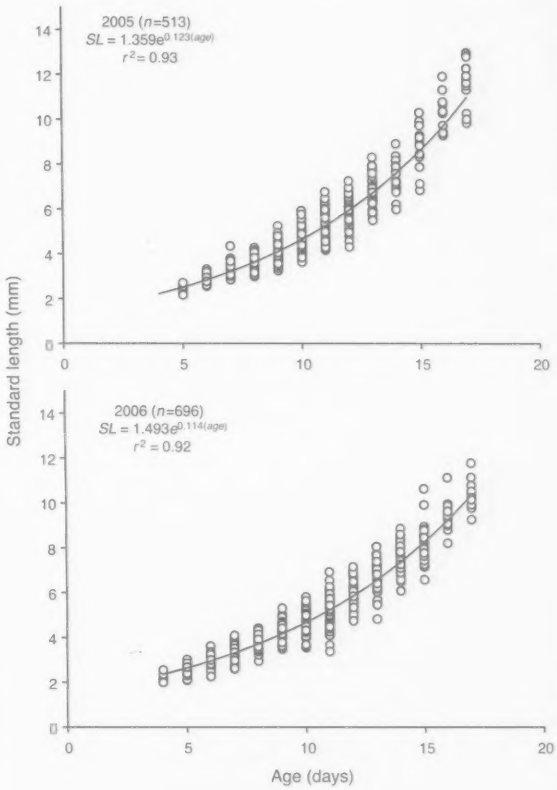

Figure 3

Size-at-age relationships of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Age in days was determined from otolith microstructure analysis. Exponential equations are given.

Spatial variation in growth of sailfish was limited despite elevated densities of sailfish larvae within fronts. The general lack of growth variation in sailfish among oceanographic features is somewhat unexpected given that cyclonic and frontal features often display increased primary productivity relative to anticyclones (Grimes and Finucane, 1991; Biggs, 1992) and that growth variation during early life is influenced by primary productivity and prey availability (de Vries et al., 1990; Wexler et al., 2007). The lack of variation in growth among oceanographic features may be attributed to the fact that larvae in the northern Gulf likely spend time in multiple oceanographic features during early life. Oceanographic currents in this region have been observed to have speeds up to 0.8 meters per second (69.1 kilometers per day) (Govoni and Grimes, 1992), and higher velocity currents have been recorded within the Loop Current (1.0 meters per sec-

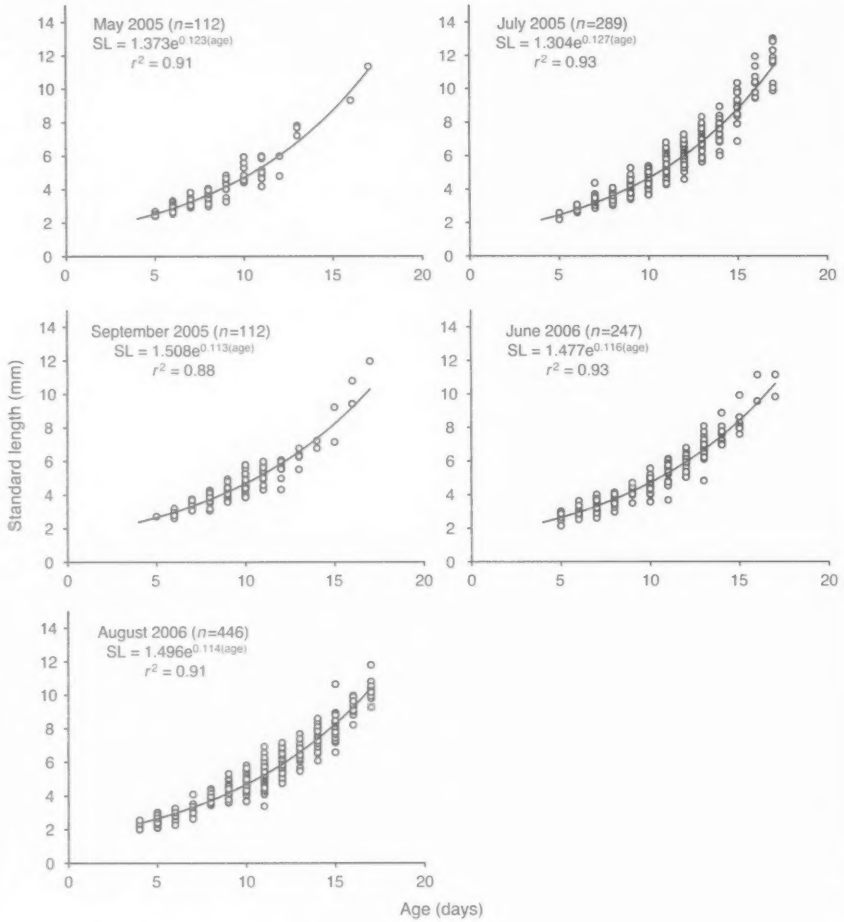

Figure 4

Size-at-age relationships of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006 arranged by survey. Age in days was determined from otolith microstructure analysis. Exponential equations are given.

Table 5

Instantaneous weight-specific growth (G) and mortality (Z) coefficients of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Percentage per day was calculated from instantaneous growth and mortality coefficients. The G:Z index of stage-specific production potential is also shown.

Year	Survey	G	%/day	Z	%/day	G:Z
2005	May	0.371	44.9	0.285	24.8	1.30
	July	0.378	45.9	0.228	20.4	1.66
	September	0.347	41.5	0.345	29.2	1.01
	All surveys	0.371	44.9	0.288	25.0	1.29
2006	June	0.351	42.0	0.344	29.1	1.02
	August	0.347	41.5	0.381	31.7	0.91
	All surveys	0.347	41.5	0.394	32.6	0.88

ond; Vukovich and Maul, 1985), which indicate that planktonic larvae may encounter multiple oceanographic features during their planktonic larval duration. Further, pelagic larvae from broad oceanic areas have been reported to accumulate within frontal zones (Richards et al., 1993; Bakun, 2006), making it difficult to determine where individuals spend the majority of their lives and therefore, in which feature(s) most of their early growth occurs.

Estimated growth of sailfish in the Gulf (g=0.113 to 0.127) varied temporally and rates were comparable to or slightly slower than those reported for sailfish in the Straits of Florida (g=0.130 to 0.146; Luthy et al., 2005; Richardson, 2007; Richardson et al., 2009a) and blue marlin from the Bahamas (g=0.098 to 0.125; Serafy et al., 2003; Sponaugle et al., 2005) and the Straits of Florida (g=0.089 to 0.114; Sponaugle et al., 2005; Richardson, 2007). Observed differences in growth among studies are minor and similarities are not unexpected because the timing of collections and environmental conditions between the regions were comparable. Sampling in the Straits of Florida was conducted between April and September in waters ranging from 26.1°C to 30.6°C (Luthy et al., 2005; Richardson, 2007). This range of temperatures is similar to temperatures present in the Gulf during our May to September sampling period (26.4–30.4 °C). Moreover, observed ranges in salinity were nearly the same between the Straits of Florida (34.0–36.7 ppt) and Gulf (35.2–36.5 ppt). Temporal variations in growth of marine larvae have been shown to be correlated with temperature (Rilling and Houde, 1999), and the most rapid growth of sailfish larvae was observed during July 2005 when the warmest mean temperature was reported. Nevertheless, the second fastest growth rate for sailfish was observed during May 2005 when the lowest mean temperature was reported. Thus, other factors known to affect growth, such as density of conspecifics or prey availability (Jenkins et al., 1991; Lang et al., 1994; Wexler et al., 2007), may be responsible for observed variations in growth of sailfish larvae.

Although intra-annual differences in mortality were limited, losses were substantial throughout the early life interval examined (Z=0.23 to 0.38). Daily instantaneous mortality rates reported in our study are 10–45% lower than mortality rates for sailfish and blue marlin larvae from the Straits of Florida and Exuma Sound, Bahamas (Richardson et al., 2009a). However, the losses reported in our study are comparable to those of other pelagic larvae, such as bluefin tuna (*Thunnus thynnus*) (Z=0.20; Rooker et al., 2007), yellowfin tuna (*Thunnus albacares*) (Z=0.33; Lang et al., 1994), and members of the suborder Scombroidei, which includes tunas, billfishes, and the barracuda *Sphyraena barracuda* (Z=0.34; Houde and Zastrow, 1993). Predation has been observed to be a major cause of mortality during the early life interval of pelagic species (Leggett and Deblois, 1994; Houde, 2002) and it may be responsible for high losses of sailfish larvae. Recent studies indicate that istiophorids are preyed upon by conspecifics and congeners (Llopiz and Cowen, 2008; Tidwell, 2008) and, if so, cannibalism or predation pressure by other istiophorids may represent an important source of mortality for sailfish during early life.

Observed $G:Z$ ratios were greater than 1.0 during all but the August 2006 survey, indicating conditions were likely favorable for production during the life stage examined. Houde and Zastrow (1993) reported a mean $G:Z$ ratio of 0.89 for marine fish larvae (pooled across several taxa), which is lower than the range reported in our study for sailfish (0.91–1.66). However, indices reported for individual species or taxonomic groups ranged from 0.26 to 2.42 for larvae abundant in upwelling and shelf zones, indicating wide-ranging stage-specific production potential for pelagic fishes. Collection of larvae peaked in July and it is possible that increased $G:Z$ coincided with increased temperature or prey availability, both of which have been

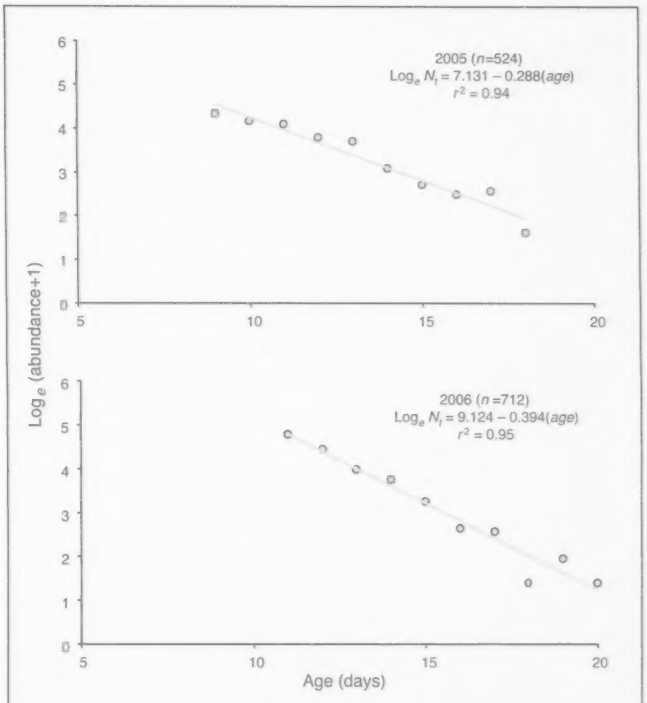

Figure 5

Regression plots of log$_e$ (*abundance*+1) on age for ten-day cohorts of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Regression equations and plots are arranged by year.

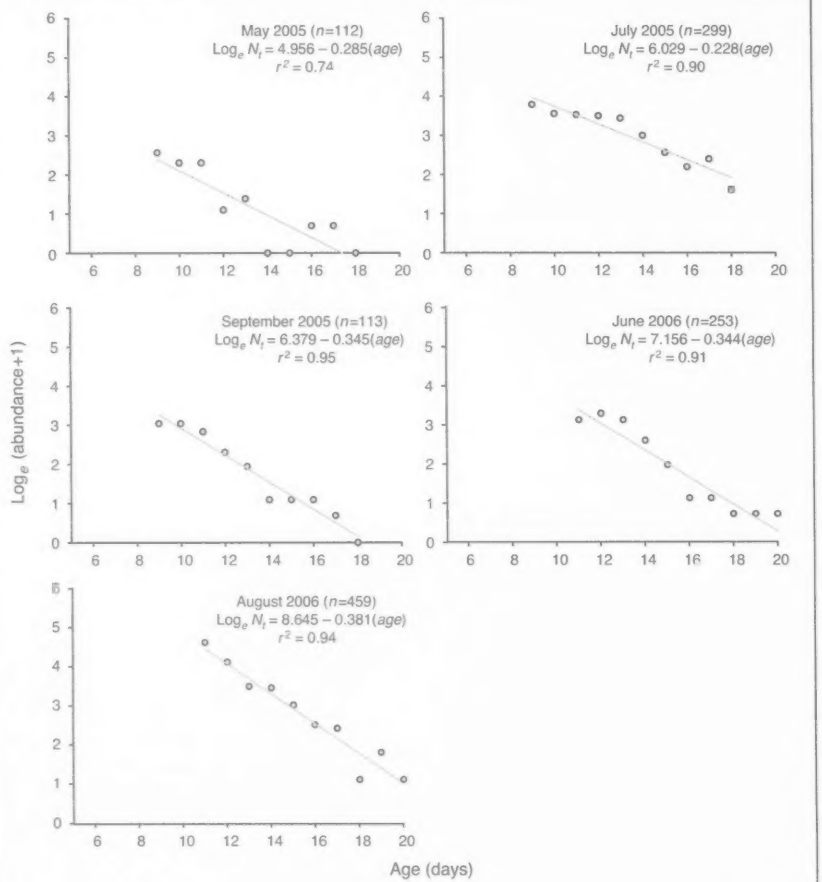

Figure 6

Regression plots of log$_e$ (*abundance*+1) on age for ten-day cohorts of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 and 2006. Regression equations and plots arranged by survey.

shown to increase stage-specific production potential (Rilling and Houde, 1999).

Hatch dates of sailfish larvae collected in this study indicate that spawning is protracted in the northern Gulf and peak activity occurs during July. To date, sailfish spawning has not been documented in the northern Gulf, but sailfish are known to have protracted spawning in other regions of the Atlantic and Pacific oceans (de Sylva and Breder, 1997; Chiang et al., 2006; Richardson, 2007). Although the timing of sampling likely influences hatch-date distributions of sailfish in the Gulf, resulting in a multimodal distribution, spawning has been shown to occur from May to September in the western North Atlantic Ocean (de Sylva and Breder, 1997) and from April to September in the eastern Pacific (Chiang et al., 2006), corresponding to the spawning range observed in this study. Additionally, data from studies indicate that peak spawning occurs in mid to late summer because increased frequencies of mature ovaries have been observed in sailfish landed in July and August (de Sylva and Breder, 1997; Chiang et al., 2006; Richardson et al., 2009a).

Questions remain regarding the specific factors regulating observed variations in distribution, growth, and mortality of sailfish, as well as the extent of spawning in the northern Gulf. Regardless, high densities and broad distributions of larvae combined with rapid growth and high production potential indicate that sailfish larvae spawned or hatched in the northern Gulf potentially contribute to Atlantic sailfish populations. This study provides strong evidence that the northern Gulf serves as an important spawning and nursery habitat for Atlantic sailfish.

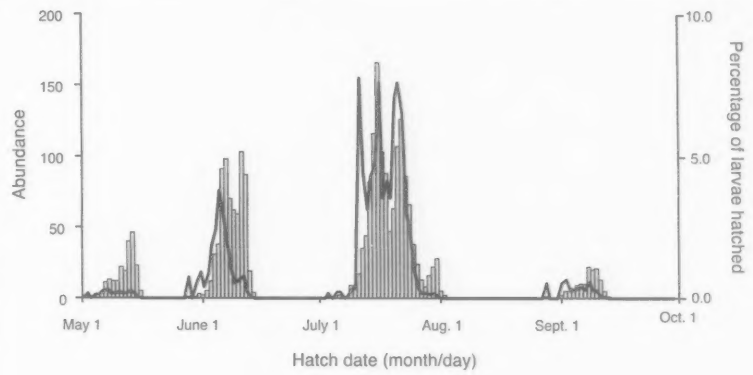

Figure 7

Hatch-date distribution of sailfish (*Istiophorus platypterus*) larvae collected from the northern Gulf of Mexico in 2005 (n=1037) and 2006 (n=1317) (gray bars). Larvae were pooled and arranged by month and day. Hatch dates were determined by subtracting age from catch date. Otolith-derived ages were used when available; remaining ages were predicted by applying age-length key. The mortality-adjusted hatch-date distribution as a percentage of hatching events per day (solid line) is also shown.

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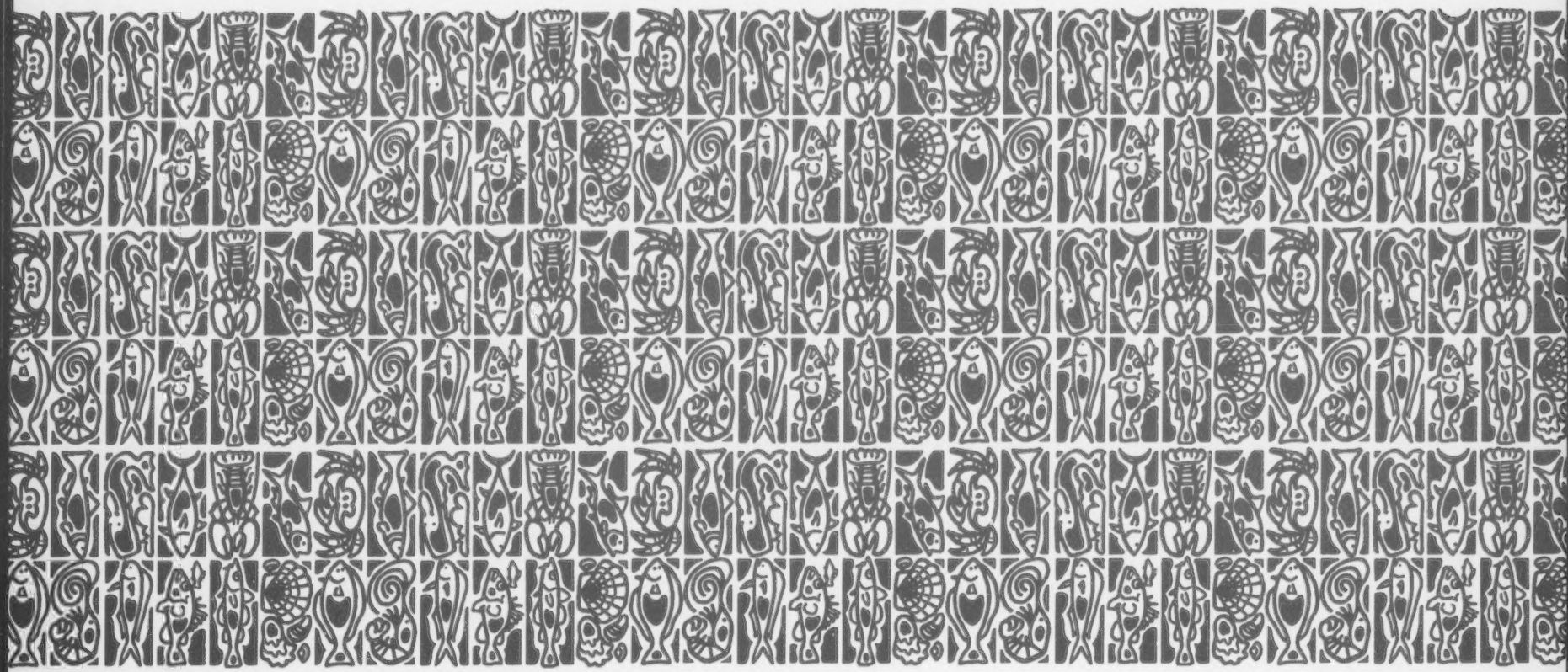

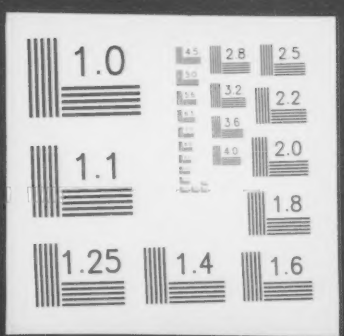
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